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BIOLOGY AND IMMATURE STAGES OF PSEUDOMETHOCA F. FRIGIDA, WITH NOTES ON OTHER SPECIES (HYMENOPTERA: MUTILLIDAE)

By

D. J. BROTHERS

Vol. 50, No. 1, pp. 1-38 August 28, 1972

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Biology and Immature Stages of *Pseudomethoca f. frigida*, With Notes on Other Species (Hymenoptera: Mutillidae)

D. J. Brothers

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Biology and Immature Stages of *Pseudomethoca f. frigida*, with Notes on Other Species (Hymenoptera: Mutillidae)[1]

D. J. Brothers

ABSTRACT

The biology of *Pseudomethoca f. frigida* (Smith) is described in detail, based on observations made in eastern Kansas in the field and the laboratory. Adult females are effectively excluded from the burrows of the host, *Lasioglossum zephyrum* (Smith) (Halictidae), by the guard bees, but successful entry is usually made when the burrow is unguarded. Once inside a nest, the mutillid is unmolested by the bees and remains for a long time, ovipositing in many cells. Female mutillids may consume one or more host pupae or prepupae during this time. Prior to oviposition the mutillid locates and removes the plug to a cell. The contents of the cell are then investigated with the antennae and the sting, and, if all the provisions have been consumed, an egg is laid anywhere in the cell. Host pupae are paralyzed, but prepupae are not. The mutillid recloses the cell with a plug of soil. The egg hatches after about 100 hours. The larva has five instars and feeds externally, consuming the entire host. About 110 hours after eclosion cocoon spinning is initiated. Defecation takes place soon after the cocoon is completed. If there is no diapause, the molt to the pupa occurs about 70 hours after defecation. The pupal stage lasts about 280 hours in the male and 320 hours in the female. After the molt to the adult, the mutillid remains in the cocoon for about 30 hours, and then chews through the cocoon and cell plug. Mating may occur immediately after emergence from the host nest. The male grasps the base of the female's abdomen with his mandibles prior to actual genital union which lasts about 15 seconds. Mated females rapidly cease to be attractive to males. In Kansas *P. f. frigida* is multivoltine, and overwintering occurs as prepupae.

The external morphology of the immatures of *P. f. frigida* is described. The egg is simple. Each larval instar has 13 postcephalic segments and 10 pairs of spiracles, the 2nd pair being much reduced. The form of the antennae, mandibles and spiracles varies with the instar. The pupae are similar to the adults but are spinose, especially on the abdomen. Some sutures are visible on the dorsum of the mesosoma in the female pupa and the sting is exserted and curved dorsally over the metasoma.

A summary of unpublished observations by Cottrell on the biology of *Dasymutilla bioculata* (Cresson) in Minnesota is presented. In this species the female gnaws a hole in the bembecine host cocoon and oviposits in the cocoon only after the host has defecated. The oviposition aperture is sealed by a salivary secretion. The egg hatches after about three days. Although Cottrell observed four larval instars, there are probably five. Spinning begins about ten days after hatching. The pupal stage lasts about 10 to 12 days. *D. bioculata* is usually univoltine but some individuals may diapause (as prepupae) for more than one season. Low temperature is not necessary to break diapause in all prepupae. Mating takes place soon after emergence, and the male does not grasp the female with the mandibles. Copulation lasts about 20 seconds. Males do not persist in copulation attempts with previously mated females.

INTRODUCTION

Despite the size of the scolioid family Mutillidae (4,000+ described species), knowledge of the biology of members of this family is scanty. Detailed biological information has been published for *Smicromyrme rufipes* (F.) (Crèvecoeur, 1930; Maréchal, 1930), three species of *Sphaeropthalma (Photopsis)* (Ferguson, 1962) and to a lesser extent for *Mutilla europaea* L. (Hoffer, 1886; Jordan, 1935) and *Chres-*

[1] Contribution number 1471 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66044.

tomutilla glossinae (Turner) (Lamborn, 1915, 1916; Heaversedge, 1968, 1969a & b, 1970). Additional brief observations on mating, host records and other such biological information are mostly hidden in the literature on other insects with which Mutillidae are associated.

Mutillidae are parasitic on the resting stages (usually the prepupa or pupa) of other insects, including aculeate Hymenoptera, Coleoptera, Diptera (Mickel, 1928) and Lepidoptera (Seyrig, 1936; Olsoufieff, 1938). There is an ambiguous record which apparently indicates parasitism of diapausing adult Pentatomidae (Hemiptera) (Mellor, 1933), although in this case the mutillid was doubtless hyperparasitic through a tachinid fly, since Morris (1930) reported that the tachinid parasites of this bug were subject to severe parasitism. Invrea (1950) noted that *Smicromyrme ausonia* Invrea was hyperparasitic on an isopod crustacean through a sarcophagid fly. Host records exist for less than five percent of the species of Mutillidae, and nothing is known of the hosts of five subfamilies (Eotillinae, Typhoctinae, Apterogyninae, Pseudophotopsidinae and Rhopalomutillinae).

In view of the meager knowledge of the biology of Mutillidae, a detailed study of the life history and biology of *Pseudomethoca f. frigida* (Smith) was conducted in connection with rearing experiments on its host, *Lasioglossum zephyrum* (Smith). A summary of unpublished investigations on *Dasymutilla bioculata* (Cresson) by Cottrell (1936) is also presented.

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The assistance of Mr. Dwight R. Kamm and Mr. Edward M. Barrows in the field is gratefully acknowledged. This study would not have been possible without the use of facilities primarily involved in studies (supported through National Science Foundation Grant GB 8588 X) by Dr. Charles D. Michener on the origin of sociality in halictine bees. This paper is thus a by-product of that grant. Thanks are also due to the following persons for their comments on parts of or the entire manuscript: Dr. C. E. Mickel, Tucson, Arizona; Dr. C. D. Michener, Dr. P. D. Ashlock, Mr. W. L. Overal, and Mr. G. Gordh, all of The University of Kansas. Thanks are also due to Mr. R. G. Cottrell, Valley Center, California, and Dr. A. C. Hodson, Head of the Department of Entomology, Fisheries and Wildlife at the University of Minnesota, St. Paul, for permission to include a summary of Cottrell's thesis. Portions of this study were undertaken during tenure of a traineeship from the National Science Foundation awarded through the Committee on Systematic and Evolutionary Biology at The University of Kansas.

STUDIES ON *PSEUDOMETHOCA FRIGIDA FRIGIDA* (SMITH)

Materials and Methods

Field observations on adults of *P. f. frigida* were made at three nesting sites of *L. zephyrum* near Lawrence, Kansas; two of these sites were banks along small streams which dried up periodically and the third was along the banks of the Wakarusa River, the principal site at which Batra (1966; fig. 3) studied *L. zephyrum*. Live adults of *P. f. frigida* were brought into the laboratory for observations on mating and activity within the host burrows in artificial nests of *L. zephyrum*. These consisted of a pair of glass plates separated by a layer of soil in which the bees constructed burrows and cells (see Michener and Brothers, 1971). Nests containing cells with immatures in various stages of development, and from which the adults had been removed, were kept at approximately 22° C. The "windows" in the sides of the cells were enlarged by removal of some soil around the cells. A female of *P. f. frigida* was intro-

duced into the burrow and the nest was sealed to prevent her escape. The nests were kept in the dark as much as possible to simulate natural conditions; it had previously been found that females of *Dasymutilla bioculata* would oviposit in cocoons of the bembecine hosts more readily in the dark (Cottrell, 1936). Each nest was inspected at intervals of 30 minutes or less. When a mutillid was noticed working in the region of a cell, her activity was examined under a stereo-microscope. Observations and measurements of the immature stages were made every few hours at magnifications of 25× and 50×. Experiments involving the interactions of bees and mutillids were performed by introducing mutillids into active artificial nests.

Details of the life history and behavior were obtained from a varied number of observations. Interactions between mutillids and bees in the field were observed upward of 20 times, and mutillids were introduced into active artificial nests on 12 occasions. At least 20 introductions were made into four different artificial nests containing immatures only, but observations on host-feeding were made on only one mutillid and reactions to cells with contents unsuitable for oviposition were noted only about five times. The complete oviposition sequence was observed three times, although incomplete observations were made on eight additional ovipositions or other reactions of mutillids to cells with contents suitable for oviposition. General aspects of the development of immatures were noted on 21 individuals and detailed notes were made on seven males and one female and an additional female pupa. Successful mating was observed twice in the laboratory and eight unsuccessful attempts were noted.

Since larvae vary considerably in size, depending on degree and manner of preservation and on age, the descriptions of the larvae are based on a single individual of each instar described. The proportions derived from the measurements, especially those of the more rigid structures, should, however, be relatively constant for each instar. The terminology used in the larval descriptions is based on that used by Michener (1953) and Evans (1965), with the format approximately following that of Evans for easier comparison with his descriptions of larvae of the related family Tiphiidae.

Outline of Biology of Host, *Lasioglossum (Dialictus) zephyrum* (Smith)

The host, *L. zephyrum*, is a small sweat bee (Halictidae, Halictinae), individuals being 5-7 mm long. Mated, overwintered queens establish new nests in early spring. Each queen usually excavates her own nest, constructing and provisioning a few cells and laying an egg in each one. The queen then becomes inactive until the first brood emerges a few weeks later. Subsequent broods ultimately replace the overwintered queens but colonies continue during the entire summer, the number of bees in each nest increasing as the season progresses. There is a gradation between mated, queenlike individuals and unmated workers with undeveloped ovaries. When two or more bees occupy a single nest, one usually remains at the entrance and acts as a guard, preventing intruders from entering the nest. Burrows are more or less at right angles to the surface of the stream or river bank and may form rather extensive aggregations. At the end of the summer most of the young females mate and overwinter in the old burrows. As in all halictines, the larvae do not spin cocoons, the pupae lying naked in the cells. For further details of the biology of *L. zephyrum* see Batra (1966) and Michener *et al.* (1971).

Outline of Life History of *Pseudomethoca f. frigida*

P. f. frigida is a small mutillid (Sphaeropthalminae), 4-6 mm long, with brown, wingless females (Fig. 1) and black, winged, males (Fig. 2). Adults emerge from pupae in late spring and females enter the burrows of the hosts which are various species of halictine bees, commonly *L. zephyrum*. The mutillid is usually repulsed by a guard bee at the entrance to an active burrow, but readily enters an unguarded burrow. After successful entry, a female mutillid locates closed cells and feeds on one or more prepupae or pupae of the host. The mutillid oviposits in cells containing pupae or larvae which have finished feeding, the egg being laid anywhere in the cell which is then resealed. The egg hatches in about 100 hours and the larva feeds externally on the host, often changing its position and making numerous feeding punctures. There are five larval instars. About 110 hours after eclosion and once the host has been consumed, the cocoon is spun and defecation occurs. During spring and summer pupation takes place about 150 hours after the start of cocoon spinning; in autumn prepupae diapause, pupation occurring the following spring. The pupal stage lasts about 280 hours for males and 320 hours for females. After molting, the adult remains in the cocoon for about 30 hours before chewing through the anterior end of the cocoon and the plug of the cell. Mating takes place soon after emergence from the burrow.

Invasion of Host Burrows

Adults of *P. f. frigida* emerge from the pupae slightly later than their hosts, starting in late April or early May. At first the mutillids are rare, but they are found in increasing numbers at the nesting sites of *L. zephyrum* as the season progresses. Although the females may become quite common during the summer at some sites, the males are encountered much more rarely. The wingless females search the river or stream banks more or less randomly for the burrows of the bees, continuously vibrating the antennae and running over the surface of the soil, investigating irregularities and especially small holes. Although movement is apparently random, the mutillids tend to work their way up the surface of the bank. When a mutillid reaches the top, it walks along the bank and comes down a short distance. Since the burrows of the bees tend to be concentrated in the top meter of the bank, any tendency for the mutillids to move upwards to this region will increase the likelihood of their encountering the host burrows.

When a mutillid approaches within a few centimeters, the guard bee often partly emerges from the burrow. The bee faces the intruder, swivelling around if the mutillid walks past (see Batra, 1966; fig. 25). If the mutillid approaches closer, the bee may bob in and out of the burrow entrance, snapping its mandibles open and shut. If the wasp approaches within about one centimeter, the guard usually retreats, turns around just inside the burrow entrance and blocks the constricted entrance with the apical terga of the metasoma, effectively sealing the burrow. Under such circumstances the mutillid may try to squeeze past the guard and may even attempt to dig past. It is usually unsuccessful, and after a few seconds it searches elsewhere.

Sealing of the burrow entrance in this way is common in most species of halictines in which more than one bee occurs in a nest, and similar responses to *P. f. frigida* have been seen in *Lasioglossum imitatum* (Smith) (Michener and Wille, 1961) and *L. versatum* (Robertson) (Michener, 1966). In Ontario, Knerer and Atwood (1967) found that *P. f. frigida*

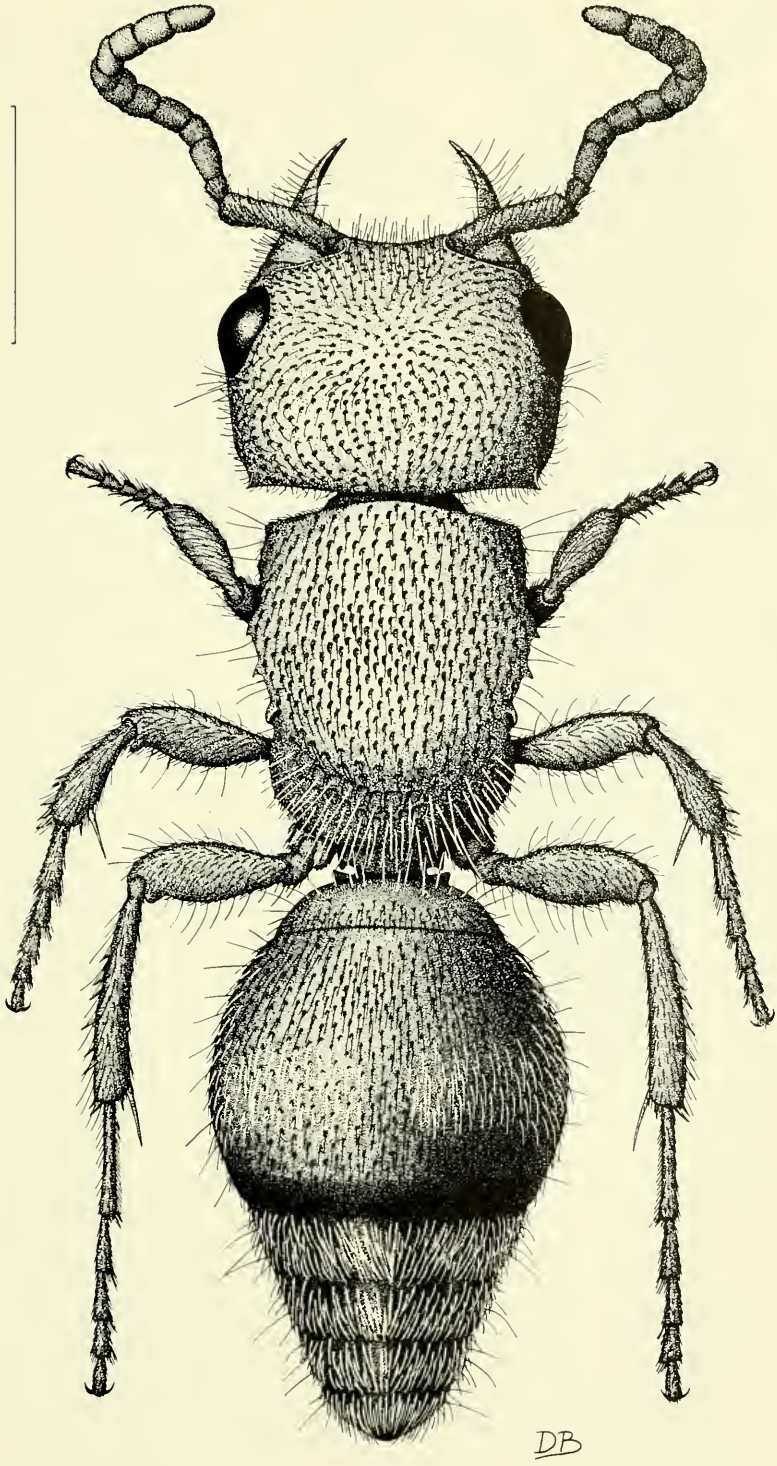


Fig. 1. *Pseudomethoca f. frigida,* adult ♀, dorsal view. Scale=1.0 mm.

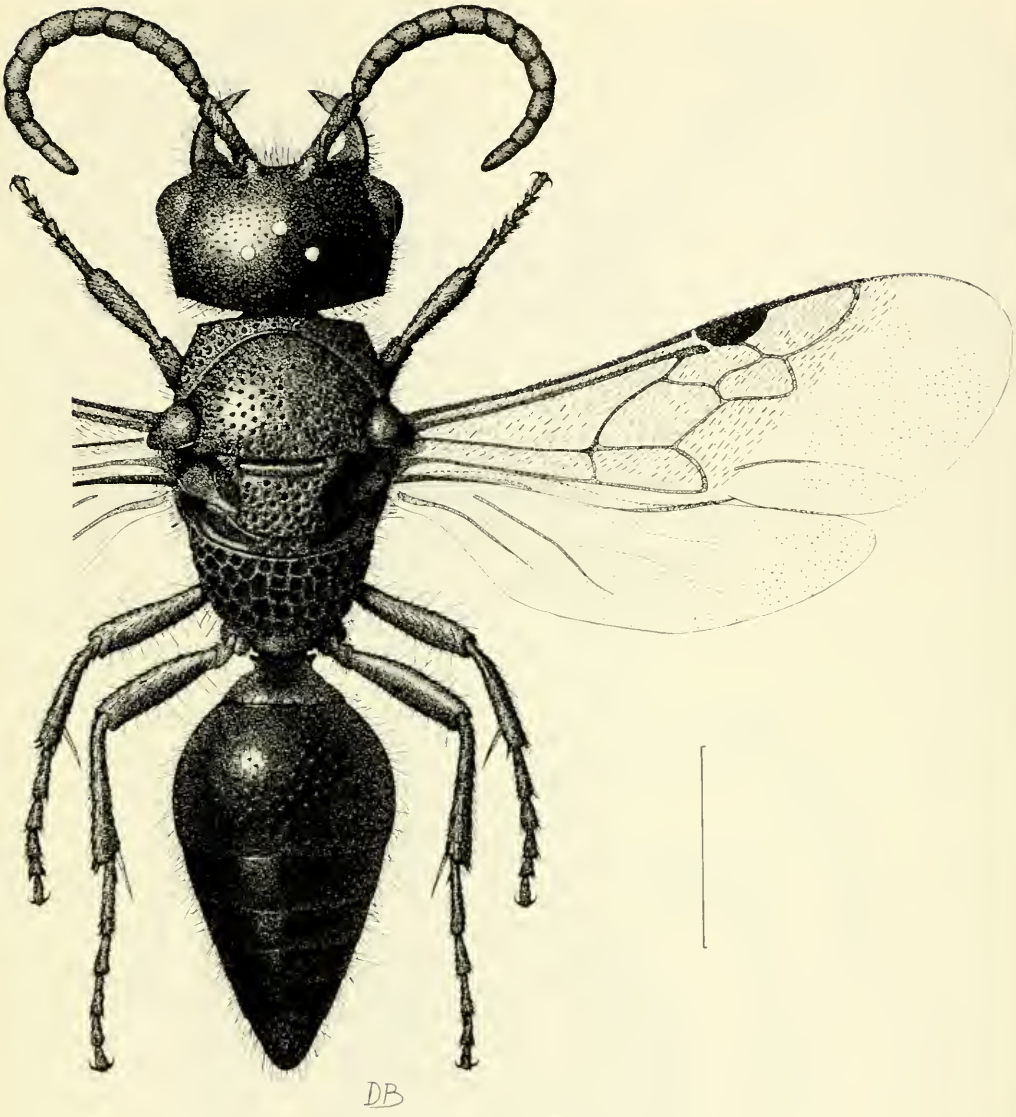


FIG. 2. *Pseudomethoca f. frigida,* adult ♂, dorsal view. Scale=1.0 mm.

"overpowers" the guards of *L. cinctipes* (Provancher) at the burrow entrance and closes the nest from the inside. By contrast, Ordway (1964) found in *Augochlorella striata* (Provancher) and *A. persimilis* (Viereck), that the guards apparently do not hinder the entrance of female mutillids [*P. f. frigida* or *Myrmilloides grandiceps* (Blake)].

Sometimes the guards of *L. zephyrum* attack a female of *P. f. frigida* if it approaches within about one centimeter of the burrow entrance. The guard is much more likely to attack a mutillid if it has repelled another a short time previously. In about 20 observations in the laboratory during which mutillids were held in forceps and presented to guards, the initial reaction was usually blockage of the burrow. If the mutillid was presented a second time, after the guard had turned around, the reaction was usually attack. A

few guards could not be stimulated to attack, but always blocked the burrow. These bees had usually been working down in the nest and had replaced the original guard if it had been removed when it attacked the mutillid. There was a tendency for such "reluctant" bees to be queens.

When a bee attacks a mutillid, it leaves the burrow suddenly and pounces on the intruder. A second bee usually replaces the guard at the burrow entrance. The attacking bee holds the mutillid with its legs and attempts to bite it, but apparently does not try to sting the wasp, an act which would be ineffective because of the toughness of the mutillid's integument. The mutillid apparently does not usually retaliate, since neither biting nor attempts at stinging the bee were seen. Because the burrows are usually in a near-vertical bank, the combatants roll to its bottom, after which the bee releases its hold on the mutillid and flies back to the burrow. If the nest is closer to level soil, the fighting bee and mutillid may roll around on the surface for a longer period. Batra (1965) noted that fights on horizontal ground may last as long as three minutes. Melander and Brues (1903) recorded "ferocious battles" between *P. f. frigida* (as *Mutilla canadensis*) and *"Halictus (Chloralictus) pruinosus"* (probably *L. zephyrum*; Michener, pers. comm.). Although Batra (1965) found no instances of the bees or the mutillid being injured, Melander and Brues (1903) stated that some of the bees were killed and Krombein (1938) found that a female of *P. f. frigida* had been "greatly weakened" by attacks from guard bees. Lin (1964) observed at least one instance in which a bee was apparently stung to death by *P. f. frigida*. During the present study a single guard was apparently killed by a mutillid, but the means by which this was effected could not be ascertained, although stinging seemed the most likely.

The stimulus for defense of the nest by a guard bee is apparently chemical. If forceps with which a mutillid had recently been held were placed near a guarded burrow entrance, the guard reacted in the same way as if the intruder were a mutillid; if a clean pair of forceps was used, no such reaction was elicited. On a few occasions, in the field as well as in the laboratory, it was observed that a bee which had just been fighting with a mutillid was prevented from entering the nest by the replacement guard. In one case the bee was allowed back in the nest only after about five minutes. Melander and Brues (1903) noted similar occurrences. Apparently the bee becomes contaminated with the scent of the mutillid during the fight, and is accepted only when this scent has dissipated.

The obstacles encountered by *P. f. frigida* in invading a nest of its host are similar to those experienced by other mutillids which are parasitic on social or colonial insects. Small mutillids are repulsed by the guards of *Pseudagapostemon divaricatus* (Vachal), a communal halictine in Brazil (Michener and Lange, 1958). Ferton (1898) observed a female of *Myrmilla capitata* (Lucas) attempting to enter a closed nest of *Lasioglossum malachurum* (Kirby) by digging a hole at the base of the turret around the nest opening. At the same time two female bees returned to the nest and attacked the parasite, ineffectually biting and trampling it. Ferton also observed that *Myrmilla bipunctata* (Latreille) attacked the closed nests of the halictines in the same way, but, early in the season when each burrow was occupied by only one bee, the mutillid avoided the nests in which a bee was present and entered those from which bees were absent. Knerer (1969) confirmed Ferton's observations on *L. malachurum*,

but also found that guarding was so well developed in this species that a small colony could be completely eradicated before a female of *Myrmilla* gained entry to the nest, in contrast to Ferton's observation of a lack of aggression by the mutillid. Knerer found that the mutillids dug their own tunnels to bypass the hard, cement-like tube at the entrance to the burrow, or waited until the rain softened it (see Knerer, 1969; fig. 3). In Australia, Rayment (1947) found that mutillids avoided nests where a female of the halictine *Lasioglossum fulviventre* (Friese) was present, but would readily enter nests that were unattended. Sometimes a mutillid would be chased by a bee.

Although bembicine wasps are not social, they often form dense aggregations and females of *Bembix* have been seen pursuing females of *Dasymutilla* and *Timulla* until the mutillids left the area (Evans, 1957: 135, 166). In contrast to these instances, and to the violent reaction on the part of species of *Bombus* to invasion of the nest by a female of the socially parasitic bee, *Psithyrus,* Hoffer (1886) never saw a single fight between the host bumble bees and a female of *Mutilla europaea,* although Miyamoto (1963) reported on the workers of *Bombus ignitus* Smith expelling a female of *Mutilla europaea mikado* Cameron from the nest.

Since the guard bees are usually effective at excluding mutillids from the nests of *L. zephyrum,* a mutillid is successful at entering a burrow only in exceptional circumstances, mainly when the entrance is left unguarded. Burrows containing a single bee may be more susceptible to invasion by mutillids than are colonies, since the lone occupant has to leave the burrow to forage and also has to leave the entrance unguarded when extending the burrow and making cells. When guarding, such a bee will often not attack a mutillid, but usually blocks the burrow entrance.

An instance of successful penetration which was observed in the field resulted from interference by a male bee. As a female of *P. f. frigida* was approaching a burrow, the guard came partly out of the burrow. At that moment a male bee pounced on the guard and the pair of bees tumbled down the bank. During the short period that the guard was absent, and while there was no replacement guard, the mutillid found and entered the burrow.

Lin (1964) observed successful penetration of a nest by *P. f. frigida* on a single occasion, when there was no replacement guard to block the burrow while the guard was fighting with the mutillid on level ground. The mutillid reached the burrow before the bee was able to return. Such lapses in the guard system are less hazardous for colonies in stream banks, since the mutillid has to climb up the bank again after it and the attacking guard have rolled to the bottom. The bee is able to fly back.

Once a mutillid has penetrated the constricted burrow entrance, it is relatively unmolested and can get past any other bees in the burrow. Effective blockage of the burrow can be made only at a constriction where the metasoma of a bee can seal the entire burrow. *L. zephyrum* makes only one constriction in the burrow, at the entrance, but there may be up to three additional constrictions at intervals along the burrow above the first cells in some species, such as *Lasioglossum laevissimum* (Smith) in Colorado (Michener, pers. comm.). In such burrows parasites are probably more effectively excluded than in *L. zephyrum,* since the burrow can be blocked by a bee at each constriction.

The mutillid works its way to the bottom of the burrow, and often starts digging there. This may not always be the case under natural conditions, since observations on behavior inside nests could be made only by introducing mutillids into

active, artificial nests. In these experiments the mutillid was first attacked by a varying number of guards, each of which was removed. The mutillid was then introduced into the nest where the reactions of the remaining bee(s) were observed. In six nests involving seven bees, the bees did not touch the mutillid although they showed some agitation when the mutillid ran to the bottom of the burrow, but they usually started guarding. In two other nests containing one working bee each, the bee did molest the mutillid to a slight extent, this usually involving pushing the mutillid with the tip of the metasoma, although one of these did try to bite the wasp and a few times appeared to attempt to sting it. In a different nest, however, the single remaining bee (the queen) attacked a mutillid that was introduced into the burrow and tried to bite it. The pair rolled down the burrow a short distance and after about 30 seconds the mutillid freed itself and ran to the bottom of the burrow. The bee followed, then turned around and began pushing on the mutillid with the tip of the metasoma. After a few pushes the bee left and ran to the burrow entrance. Every few seconds it returned to the intruder and pushed on it again. After about five minutes the bee did not approach the mutillid again, but ran around in the burrows for two minutes before it started guarding. When confronted with another mutillid at the burrow entrance, this bee did not attack but blocked the entrance with its metasoma. In a further instance the nest contained two bees, both of which were working below, the entrance having been loosely closed with soil particles. In this case the upper bee attacked the introduced mutillid for a few seconds but then started guarding. The other bee blocked the burrow with the metasoma, but it gradually retreated as the mutillid pushed on it. After about one minute the pair of insects reached the bottom of the burrow and the mutillid pushed past the bee which then went to the burrow entrance. In another case a mutillid was introduced into a nest containing three bees. It was not attacked by one but was slightly mauled by the other two which then went to the surface and began guarding. The third bee then walled off the mutillid at the end of the burrow by constructing a plug of soil about five millimeters thick just above the mutillid. Meanwhile the two guards were presented with another mutillid; both attacked, although not very readily. When the mutillid had been sealed off, the other bee went to the nest entrance and started guarding. After some hesitation this bee also attacked another mutillid.

In most cases a mutillid is thus almost entirely unmolested once it has gained entry to a nest. Even in cases where it may be walled off with a plug of soil it can easily dig its way out. Once a mutillid has been inside a nest for some time it most likely acquires the nest odor, after which it is probably entirely unmolested. A mutillid probably remains a considerable time in a nest once it has penetrated the defenses, wandering around the burrows and searching for cells. It was often found in the field that over 90% of the cells of any one nest had been parasitized, some having more than one mutillid egg, whereas none of those of an adjacent nest had been attacked. Batra (1965) also found that superparasitism was not uncommon, which reinforces the impression that a female *P. f. frigida* tends to remain in a single nest for a long time, finding and ovipositing in some of the cells more than once.

Indications of a similar lack of interaction between the bees and mutillids inside the nest were found in *Neomutilla attenuata* (Spinola), the females of which spend the greater part of the time in the burrows of *Corynura chloris* (Spinola)

(Halictinae), staying mainly near the bottom where there is the largest number of cells and leaving the burrow only to reach another (Janvier, 1933). Janvier also found a single male in the middle of a group of 46 female mutillids, most of which had presumably recently emerged and would soon disperse. De-Stefani (1886) likewise found both sexes of *Myrmilla capitata* in the burrows of *"Halictus nylanderi"* but did not record any interactions. Although the females of *Mutilla europaea* are often not attacked by the bumble bees on which they are usually parasitic, they are attacked by worker honey bees (*Apis mellifera* L.) if they invade a hive (Jordan, 1935). The mutillid retaliates by stinging the bees to death. After being in the hive for some time the mutillid apparently ceases to be molested, as was also observed by Scholz (1879). Bryant (1870) noted an instance in which a large female of *Dasymutilla occidentalis* (L.) invaded a hive in Texas and was attacked by the bees which it then stung to death.

Feeding

In the laboratory a female of *P. f. frigida* was once seen to open a cell containing a pupa and puncture the immature bee with its mandibles. The wasp then lapped up the exuding liquid. At intervals the mutillid manipulated its prey with the mandibles and then resumed lapping. After some time the mutillid left the prey without resealing the cell. She often stopped at the same cell later and resumed feeding. If adult bees had been present, they would probably have filled such an opened cell with soil. In the rearing rooms cells that had failed to produce viable young were often filled in. Because of this, a mutillid may kill and feed on a greater number of young bees under natural conditions.

Although feeding on the immatures of the host species has not previously been reported for mutillids, similar behavior by female Thynninae (Tiphiidae) was reported by Janvier (1933: 249). There are also records of female mutillids attacking and consuming the body fluids of other insects. Scholz (1879) and Jordan (1935) observed *Mutilla europaea* killing adult honey bees in the hive by malaxating the back of the neck and sucking the body fluids from the wound. Mellor (1927) described females of *Pseudophotopsis continua* (F.) killing and feeding on adults of *Bembix olivacea* (Cyrillo), attacking them in their burrows in the sand. Perhaps the most peculiar record is that of Neal (1884) who observed mutillids feeding on larvae of *Papilio cresphontes* Cramer (Lepidoptera).

A female of *P. f. frigida* was once seen to lap up some of the liquid on a pollen ball that was being consumed by a medium-sized bee larva. Although the wasp was nipped on the mouthparts by the gnashing mandibles of the larva, she did not seem to respond, but withdrew after a few seconds and reclosed the cell. In the few cases when a mutillid opened cells with tiny larvae on almost complete pollen balls or complete pollen balls with eggs, the provisions were rather dry and the mutillid did not feed on them. Since mutillids readily lap up sugar solutions in the laboratory, broken pollen balls from which a larva has fed may provide a greater stimulus for feeding because they tend to be moister than complete pollen balls.

It is also probable that *P. f. frigida* uses sugary solutions such as nectar in nature. Although none was observed doing so during the present study, Krombein (1951a) observed both sexes of *P. f. frigida* feeding on the sugary secretions of the tulip-tree scale [*Toumeyella liriodendri* (Gmelin)] in Florida, the females on the ground beneath the trees and the males

usually on the leaves. Lenko (1970) recorded females of *Traumatomutilla latevittata* (Cresson) and *Cephalomutilla distincta* Mickel disturbing cicadellids (Homoptera) on leaves, causing them to secrete honeydew which the mutillids then consumed. Invrea (1964) cited a number of cases of mutillids visiting plants infested with Homoptera. Nectar feeding is apparently much more common in male Mutillidae than in females, the males often visiting flowers (Invrea, 1964; Jacot-Guillarmod, 1951).

The females of *P. f. frigida* presumably need some source of nutrients for ripening of the oocytes (Bartlett, 1964), although individuals of this species may emerge from the pupa with some oocytes already fully developed, as was found for species of *Photopsis* by Ferguson (1962) and is possibly the case in *Chrestomutilla glossinae* (Heaversedge, 1969b). Dodson (1966) observed an unidentified female mutillid opening a cell of *Euglossa intersecta* Latreille (Anthophoridae) and apparently ovipositing within a few hours of emergence and before mating. In contrast, Cottrell (1936) found that a definite preoviposition period of up to about a month was necessary in *Dasymutilla bioculata* under artificial conditions.

Oviposition

Prior to oviposition a female of *P. f. frigida* runs along the burrows investigating the walls with its antennae, concentrating its searching in the region where the cells have been constructed. It probably locates the cells by some chemosensory means since the plugs of the cells are tamped down and smoothed off by the bees and appear indistinguishable from the burrow walls. When the mutillid has located a cell, she removes soil particles from the plug with the mandibles. As a small hole is made, the antennae are inserted into the cell. After a few minutes the hole is large enough for the entire head to be inserted. The contents of the cell are then investigated for a few seconds with the rapidly vibrating antennae. If the bee larva has not yet finished feeding, the cell is not suitable for oviposition and the mutillid usually withdraws at once and recloses the cell. If an egg were to be laid in such a cell, it would be in danger of being damaged or eaten, since the bee larva continually opens and closes its mandibles.

If the cell contains no pollen mass, i.e., if the larva has finished feeding but has not yet defecated, or more usually if the immature bee has reached the prepupal or pupal stages, the contents are suitable for parasitization. After investigating the contents of such a cell with the antennae for a few seconds, the mutillid withdraws and turns around, inserting the metasoma into the cell. If the opening in the cell plug is too small, the mutillid turns around and enlarges the opening with the mandibles. When the apical half or more of the metasoma has been inserted into the cell, the sting is protruded for up to about half its length and is partially withdrawn and extended as the mutillid probes around in the cell. The host is investigated for about two minutes with the tip of the sting and in some cases the cuticle of the host is probed a few times. The sting sometimes punctures the cuticle of the host, but in such cases only the tip penetrates. The immature bee usually does not respond to investigation by the antennae, but moves strongly when it is touched by the sting. After this investigation the mutillid partly retracts the sting and remains almost motionless but with slight jerking movements every five to ten seconds, even if it is touched by the host which may wriggle violently for some time after the mutillid stops probing. Pumping movements can be seen at the tip of the metasoma of the mutillid. After two to three minutes the

sting valves part, the egg emerges ventrally at the base of the sting, is gradually pumped out of the genital canal, and curves ventrally away from the sting. The egg may slide down along the under side of the sting and is deposited in any position on the host or on the cell wall, a type of oviposition behavior which is included in the "Chrysis type" by Iwata (1942). The egg adheres to the host and does not become dislodged even if the host moves quite violently, although it is not actually glued down.

Once the egg has been laid the mutillid withdraws slightly from the cell and gathers soil particles with the front legs and mandibles. The particles are passed to the hind legs and are packed under the ventral tip of the metasoma. The soil is tamped down with the ventral surface of the metasomal apex from the inside of the cell. As more soil is added, the hole in the plug is reduced and the metasoma is gradually withdrawn. When the metasoma can no longer be inserted through the hole, the final plugging is done entirely from the outside of the cell. The soil is then tamped down with the pygidium. The mutillid often cannot obtain sufficient soil in the immediate vicinity of the cell and moves a few centimeters down the burrow, removing particles from the walls with the mandibles. The soil is brought back to the cell by being rolled between the front legs and the mandibles. The mutillid usually backs past the cell and investigates it with the antennae, then turns around and feels for the plug with the tip of the metasoma. The plug is gradually built up and soil is also placed on the adjacent burrow walls so that the plug merges with the surface of the burrow. Once a cell has been closed by the mutillid the plug is apparently indistinguishable from the burrow walls, and is similar to that of a cell which was closed by a bee. The process of reclosing the cell is often long and may last up to about 100 minutes. This is in contrast to the host bee for which plugging of a cell takes only one to five minutes (Batra, 1964). The time observed for construction of a suitable plug was probably extended due to the artificial conditions, however, since soil was often removed by the observer from the sides of the burrows and the openings in the sides of the cells were enlarged for greater visibility. Ten to 15 minutes may be more typical for closure, as was twice observed in burrows which had not been extensively cleared. Closure is important since a parasitized cell, if left open, would be subject to destruction by the bees; no open cell naturally contains large young.

When the closure has been completed, the mutillid usually grooms itself for a few minutes and then resumes its search for cells. In at least one instance a second egg was laid 15 minutes after a mutillid had completed closure of the previous cell. Apparently most of the ovarioles may contain mature oocytes at about the same time, since one female was found to lay six eggs in 36 hours. This is confirmed by dissections of the ovaries of *P. f. frigida* (Knerer and Atwood, 1967), in which each of the six ovarioles was found to contain a mature egg.

Sometimes more than one egg is laid in a single cell (Fig. 3), the cell in such cases being reopened some time after the first egg was laid. A female of *P. f. frigida* was once observed opening a cell in which she had laid an egg on a pupa the previous day. In this case the mutillid reclosed the cell after a short investigation of the contents with the antennae and did not lay another egg. The egg had been placed on the head of the pupa and so was probably contacted by the antennae of the mutillid. Superparasitism thus possibly results only when the first egg is laid in such a position that it is not detected upon subsequent investigation of the cell contents by the

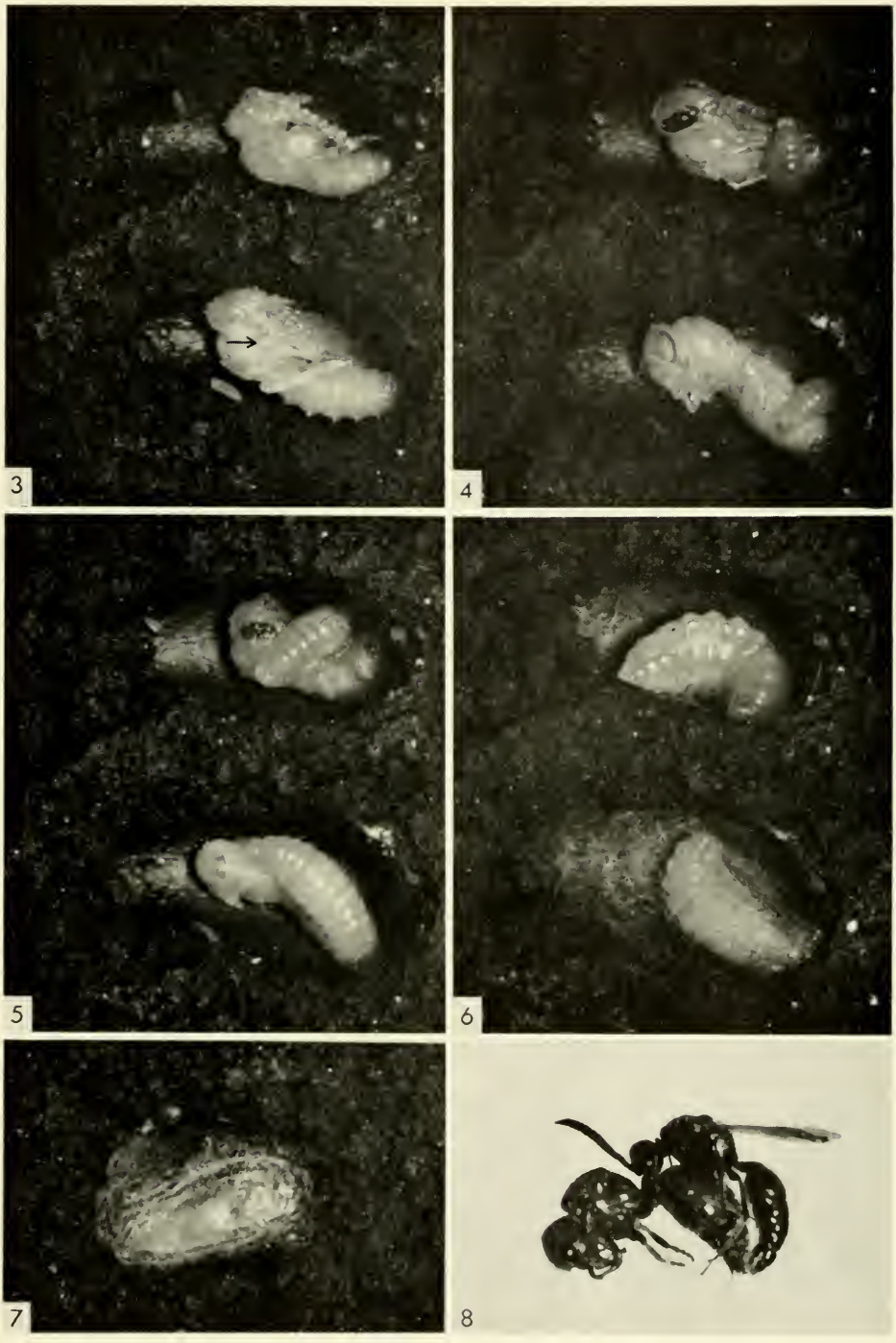
wasp, although Batra (1965) found a cell containing three small larvae and an egg. Such multiple parasitism is apparently not uncommon in the Mutillidae; it has been found in *Photopsis* by Ferguson (1962) and is the rule in *Chrestomutilla glossinae* (Heaversedge, 1969b). In contrast, Cottrell (1936) found that the females of *Dasymutilla bioculata* would not oviposit in a cocoon that had already been parasitized.

From the laboratory investigations it appears that *P. f. frigida* paralyzes the host only if it has reached the pupal stage. All of the approximately ten pupae parasitized in the laboratory remained motionless or moved only very feebly after an egg had been laid in the cell, even if they were stimulated with a dissecting needle, and most pupae found parasitized in the field showed minimal responses; unparasitized pupae always responded to stimulation with violent movement. A very small amount of venom must suffice for paralysis, since the sting was seen to penetrate the cuticle of the pupa for a mere instant. Prepupae were never paralyzed, since they all showed strong movements if stimulated after an egg had been laid in the cell. Furthermore, in some cases the prepupae molted to the pupal stage before the mutillid egg hatched, the egg remaining attached to the prepupal cuticle. Paralyzed pupae showed little or no evidence of further development such as darkening of the eyes, even if the mutillid egg were removed before it hatched. It may be that development of a pupa that has been parasitized must be prevented so as to prevent toughening of the cuticle to the point where it could not be penetrated by the mandibles of the mutillid larva; this danger is not present in the case of a prepupa. In one case a mutillid opened a cell containing a dark-eyed pupa but apparently did not penetrate the pupal cuticle with its sting, whereupon it reclosed the cell without laying an egg. Batra (1965) also concluded that prepupae of *L. zephyrum* were not paralyzed by the female mutillid, but became paralyzed once the mutillid larva had begun feeding. She did not mention the state of pupae on which eggs had been laid. In the present study it was found that prepupae were capable of some movement for as long as about two days after the mutillid larva had started feeding.

In contrast, Janvier (1933) found that *Neomutilla attenuata* parasitized only the pupae of *Corynura chloris,* the eggs being placed obliquely across the pronotum with the cephalic pole oriented towards the head of the host. The host pupae were apparently not paralyzed, since they would move the metasomal segments if touched and they would develop normally if the egg were removed before hatching. Janvier also observed that *Dimorphomutilla lunulata* (Spinola) parasitized the immatures of *Allocistertica tristrigata* (Spinola) after the hosts had spun their cocoons. The sting of the mutillid was protruded from the tip of the metasoma at the time of egg laying.

Larval Development and Cocoon Spinning

The egg of *P. f. frigida* hatches about 100 hours after laying, the first instar larva emerging through a tear in the anterior end of the chorion, which then collapses. The larva does not possess any egg bursters such as have been found in a eumenid (Cooper, 1967). If the egg was laid on the host, the larva moves around for some time before biting the cuticle of the host with its simple mandibles. It may make a number of attempts before finding a position in which a successful puncture can be made. The initial feeding site is usually on the ventral surface of the thorax, or the head or appendages in the case of a pupa, but this position varies considerably. If the egg was laid on the cell wall, after



FIGS. 3-8. Biology of *Pseudomethoca f. frigida*. **3,** eggs in cells of *Lasioglossum zephyrum*—note two eggs in lower cell, one arrowed; **4,** third (above) and fourth instar larvae—note collapsing appendages of host pupae (96 hours after Fig. 3); **5,** fourth instar larvae (29 hours after Fig. 4); **6,** fifth instar larvae starting to spin (43 hours after Fig. 5); **7,** cocoon—note supporting threads and longitudinal ridging; **8,** male attempting to mate with tethered female.

crawling around for a while the larva rears up until it is attached to the cell wall by the tip of the abdomen only. The anterior part of the body is then moved from side to side in a searching fashion, the larva projecting at right angles from the cell wall. If it does not touch the host during this searching behavior, it crawls along the wall a short distance and repeats the process. If it should touch the host, however, it attempts to apply the ventral surface of the head and thorax to the host. Once this has been accomplished the larva adheres to the host by its smooth ventral surface and releases its hold on the cell wall.

The larva changes position at each molt. During ecdysis the cuticle splits dorsally at the midline on the head and the first few postcephalic segments. The larva then crawls out of the old cuticle which adheres to the host. During each stadium the larva also changes its feeding position a number of times. Evidence for this is easily seen if it has fed on a darkening eye of the host pupa, since the feeding punctures produce colorless patches in the red eye field. The reason for these numerous changes in feeding position is not obvious, but it may be that the body fluids of the host tend to coagulate at any one puncture after some time so that a new puncture may have to be made. Similar mobility of the larvae of *Photopsis* was noted by Ferguson (1962).

The color of the larva varies, depending on the state of the host. If the host is a prepupa or pupa which has not yet started coloring, the mutillid larva is translucent white with the gut contents pale yellow. If the host is a pupa which has begun to darken and the mutillid larva has punctured a developing eye of the host, the larva appears to be pink because of its dark purple gut contents.

There are five larval instars, based on measurements of the width of the head capsule (Fig. 9), growth accelerating in each succeeding instar. The period from eclosion to final consumption of the host lasts about 210 hours. (Durations of each instar are shown in Fig. 10.) During the

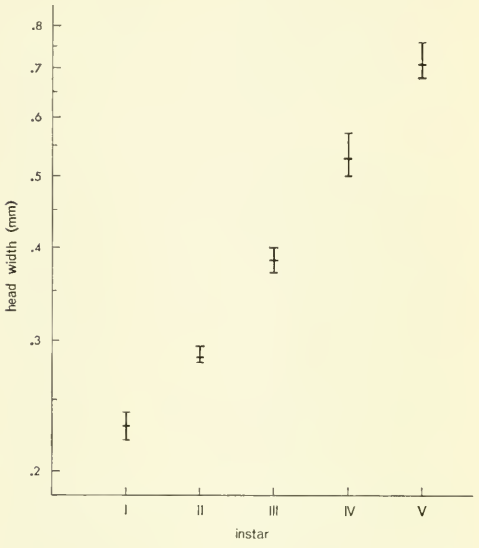


Fig. 9. Means and ranges of widths of head capsules of larvae of *Pseudomethoca f. frigida* (n=8).

first four stadia the parasite larva confines its feeding activities to puncturing the host cuticle and consuming the exuding fluids. The host gradually shrivels, the first signs of this in a pupa being the collapse of the appendages (Figs. 4-5). At the beginning of the fifth stadium of the parasite the host contains relatively little fluid and the mutillid larva uses the mandibles, which have four strong teeth, for chewing the host tissues. Final consumption of the host takes place by the mutillid larva's curling its head ventrally and chewing the rather dry scraps which are held on the ventral surface of the abdomen. After the last fragments have been consumed, the larva opens and closes its mandibles, feeling along its ventral surface as though to ensure that no morsels have been missed. In spite of this voracity small scraps of the host are sometimes left uneaten, probably because they were not found by the larva

FIG. 10. Means and ranges of developmental times between ecdyses for immature stages of *Pseudomethoca f. frigida*, ♂ below (n=7), ♀ above (n=1, 2 for pupa). A=adult; d=defecation; E=egg; L=larva; P=pupa; s=start of spinning; I-V=larval instars.

or perhaps because they were too hard. In contrast to the findings of Ferguson (1962) and Cottrell (1936) for *Photopsis* and *Dasymutilla bioculata* respectively, the larvae of *P. f. frigida* could not be induced to feed on additional host individuals if these were supplied at about the end of feeding on the original host individual.

After the host has been consumed, and sometimes before the last scraps have been disposed of, the larva starts to spin the cocoon (Fig. 6). The larva may interrupt its spinning activities in the early stages to finish off any host fragments as it contacts them. The silk is produced from the spinneret on the labium, and it usually issues as two distinct strands, one from each side of the slitlike opening. The first stage of cocoon spinning involves the apparently random laying down of silk on the walls of the cell to form a thin lining. After this the lengths of the silk arcs across the lumen of the cell are gradually increased, so that the lumen becomes somewhat reduced. When this has reached the correct size, which no doubt depends on the size of the larva and restrictions on its movements, the larva continues spinning without producing a further restriction of the lumen. The result is that the strands are laid down much closer together and the silk gradually forms an almost continuous layer which becomes the wall of the cocoon proper. When there are only minute spaces left in the wall the larva often appears to smear the silk on to the wall by applying the labium closely to it and moving about without withdrawing from the surface. The ovoidal cocoon is suspended in the cell by a network of threads, there usually being a space between the cocoon and the cell wall (Fig. 7).

Spinning lasts about 50 hours. At first the silk is white, but after a few hours it gradually becomes golden brown. This process is dependent on the presence of a certain amount of moisture. When larvae were reared in cells in dry ground, the cocoons were formed of rather loose threads which remained white; the silk turned brown within a few hours if the soil was then moistened. Such "tanning" of the cocoon is probably important for waterproofing to prevent desiccation, especially when overwintering. [Diapausing prepupae of *Myrmosula parvula* (Fox) (Tiphiidae, Myrmosinae) kept in the laboratory in damaged or untanned cocoons soon desiccated, although those kept under identical conditions in intact, tanned cocoons remained viable for several months (Brothers, in prep.).] The cocoon wall itself is papery and very thin with slight longitudinal ridges. The cocoon is not provided with a tough outer layer as is usually constructed by the larvae of *M. parvula*. A small sample of cocoons of *P. f. frigida* collected in the field measured about 5.3 × 2.1 mm, whereas a sample produced in the laboratory were about 5.9 × 2.4 mm, perhaps because of artificial enlargement of the cells in the laboratory nests.

The cocoon of *Photopsis* is ovoidal and similar to that of *P. f. frigida,* the exact method of construction depending on the size and shape of the host cell or cocoon (Ferguson, 1962). The cocoon of *Dasymutilla sackenii* (Cresson) apparently has thick walls with the emergence end rather thin, at least when formed in the cocoon of *Bembix occidentalis beutenmuelleri* Fox (Bohart and MacSwain, 1939). There is apparently a peculiar situation in *Smicromyrme rufipes,* since Crèvecoeur (1930) states that this species does not usually spin a cocoon, but sometimes does so under artificial conditions. The type of cocoon constructed by this species may, however, be similar to that of another member of the Mutillinae, *Timulla (Trogaspidia) castellana* (Mercet), which merely adds silk directly to the host cocoon,

thus thickening the walls (Brothers, in prep.).

About 30 hours after completion of the cocoon the larva of *P. f. frigida* is oriented with the head towards the plug of the cell and defecation takes place. The feces may form a strand with bead-like nodules, and often produce a slightly discolored patch at the posterior end of the cocoon, but they do not soak through the silk and cement the cocoon to the end of the cell, as occurs in *M. parvula*. The larva takes on a typical prepupal form, becoming translucent white or cream-colored. As development of the pharate pupa proceeds, a slight constriction appears just posterior to the first abdominal segment, the cuticle in the anterior region becoming taut and smooth, especially ventrally. Just prior to ecdysis the curled appendages of the pharate pupa can be seen through the cuticle on the ventral surface of the mesosoma.

It is of some interest to note that Ferguson (1962) found four larval instars in *Photopsis*, as did Cottrell (1936) in *Dasymutilla bioculata*. In *P. f. frigida* the first ecdysis may apparently take place even before feeding has started and the first and second instars are very similar, the form of the antennae in these instars differing from that in later stages, being much more elongate. Ferguson (1962) mentions that the first instar larva of *Photopsis* differs from the other instars in a similar way. It is thus possible that there are actually five instars in these other species, since the first molt is probably easily overlooked.

Pupal Development

The ecdysis to the free pupa takes place about 70 hours after defecation, if there is no diapause. Ecdysis occurs, as before, by a longitudinal middorsal split on the head and thorax. As the larval cuticle is gradually worked posteriorly, the appendages of the pupa uncurl and become turgid within a few hours. This process is probably aided by the development of a deep constriction between the first and second abdominal segments dorsally, the pupa initially being rather vermiform. The pupa attains its final shape after about 12 hours. The pupal stage lasts about 280 hours in males and 320 hours in females. During this period the coloration gradually develops in a set pattern. Ferguson (1962) found that the pattern of color development was rather specific in different species of *Sphaeropthalma (Photopsis)*.

In the female of *P. f. frigida* the first indications of pigmentation appear after about 70 hours when the eyes become pale pink. The eyes gradually darken in color until they are a dark reddish brown after about 140 hours of pupal life. There is little change for approximately another 50 hours, when the first darkening of the edges of the mandibles takes place, together with browning of the clypeal margin, the antennal tubercles, bases of the coxae and the anterior margin of the pronotum in the neck region. Darkening proceeds more rapidly from this point on, with a general browning of the body, although there tends to be slightly deeper color developed at the sutures and spiracles on the mesosoma. After the acquisition of a general pale brown color a grey coloration develops at the apices of the fore tibiae, at the apices of the mid femora, medially on the hind femora, at the apex of the second tergum and over most of the surfaces of the third to sixth metasomal terga, as well as on the entire fourth to sixth sterna. Minute black spots develop over most of the body surface at the bases of the pubescent hairs. Later the apices of the flagella become blackish and there is general darkening of the pigmentation. The pubescence becomes obvious under the pupal cuticle. About 40 hours before the adult emerges the pupal cuticle becomes wrinkled. Shortly before the final

ecdysis the pharate adult wriggles actively if it is stimulated.

In the male, the first pigmentation is also laid down in the eyes, which become pale pink after about 60 hours. The eyes and ocelli darken gradually to a reddish brown when the pupa is about 100 hours old and at about 150 hours the mandibles show the first indications of browning along the edges. At about the same time there is a tinge of brown at the neck region and at the pro-mesonotal, meso-metanotal and metanotal-propodeal sutures, as well as at the bases of the wings. A greyish tinge soon develops on the mesosoma and this gradually spreads to the metasoma, the first metasomal segment being the first to become pigmented. The pigmentation spreads distally along the metasoma, the segments first developing brownish apical margins and then progressively becoming grey. When the color is first laid down anteriorly on the metasoma the head also develops a general greyish color, with the scape becoming brownish. The grey coloration of the legs develops from the base towards the apex. The mesosoma and head and most of the metasoma then turn black, with the apex of the metasoma remaining brown and gradually becoming black. The legs become black except for the tarsi which remain brown. The flagella remain whitish even after the scapes have turned black. The wings become greyish, developing black speckles which are probably the bases of the microtrichiae. There are also many black spots over the entire body surface, as in the female, but they are much less obvious because of the black color of the cuticle in the male. About 40 hours before the final ecdysis the flagella and tarsi are greyish brown, and the pupal cuticle has begun to shrivel and wrinkle.

At the apparent end of the pupal period (see Hinton, 1971), ecdysis occurs inside the cocoon. The pupal cuticle is worked posteriorly over the body until it is pushed off the tip of the metasoma. Often scraps of cuticle remain, adhering to the mouthparts and antennae for some hours after the adult has rid itself of the rest of the cuticle. The fragments are gradually removed by the front legs.

In a very few cases in the laboratory and apparently in a single male collected as an adult in the field, the pupal cuticle had not been cleanly removed from one of the wings. As a result that wing was deformed and the mutillid could not fly. This is probably of little significance in a species which parasitizes a host which forms large aggregations, such as *L. zephyrum*, since the male mutillid does not have to fly to search for females under such conditions; running around on the bank is probably efficient enough. The deformed wing had no effect on the readiness with which such a male mated. It is possible that reduction in wing size, resulting in more efficient molting and reduced expenditures of energy, may be selectively advantageous under such conditions of host aggregation. This could eventually lead to brachyptery and finally aptery in the males of some Mutillidae. Apterous males are not uncommon in the subfamily Myrmillinae, and some species of *Myrmilla* are known to be parasitic on halictine bees. The males of *Myrmilloides grandiceps* (Sphaeropthalminae) are brachypterous, and this species is probably parasitic on similar hosts, having been collected in the nests of two species of *Augochlorella* (Ordway, 1964). Specimens of *M. grandiceps* were also collected on the banks where *L. zephyrum* was nesting during the present study.

After molting, in both sexes the adult of *P. f. frigida* remains more or less motionless inside the cocoon for about 30 hours. The cuticle hardens and the wings of males are expanded and hardened during this period, towards the end of which

the meconium is discharged in the form of small, white pellets which dry quickly. The wasp then chews through the anterior end of the cocoon and the plug of the cell and leaves the burrow.

About equal numbers of males and females were found in approximately 20 cocoons collected in the field. In the laboratory more males than females were produced, possibly because of the artificial conditions which may have inhibited fertilization of the eggs. This contrasts with the situation in *Chrestomutilla glossinae* in which Chorley (1929) found that out of a total of 1176 mutillids reared from tsetse fly puparia collected in the field, only 176 were males. In the same species Heaversedge (1969a) found that the sex ratio varied with season, the proportion of males rising at the beginning of winter and dropping in spring, but females generally outnumbered males, except in midwinter.

Mating

Mating in *P. f. frigida* probably occurs as soon as a female emerges from the burrow. Under artificial conditions a female was ready to mate as soon as she had attained the hardened condition in which she could escape from the host cell (i.e., she would not mate when teneral). Investigations were made by confining a recently emerged female with a male in a petri dish. Under such circumstances, if a male approached the female within about one centimeter he became very agitated and ran rapidly and apparently randomly in the dish, holding the wings at an angle of about 45° to the body and the substrate. The wings were vibrated rapidly in bursts and the male made short, hopping flights, usually no longer than about three centimeters. In the field similar observations were made, a male running randomly over the soil or sometimes flying just above the surface, and then speeding up his movements markedly when he approached a female and apparently sensed her presence, presumably by smell. The searching movements were then confined to within about 10 centimeters of the female. Krombein and Evans (1954) noted similar behavior in *P. frigida torrida* Krombein, in Florida.

After a short period of frantic searching the male usually contacts the female and mounts at once, climbing on to her dorsum and holding her with his legs. The male then grasps the base of the metasoma of the female in the petiolar region with his mandibles and releases his hold with the front two pairs of legs (Fig. 8); the middle legs are extended sideways. The male then prods the tip of the metasoma of the female with the partly extruded genitalia, at the rate of about one prod per second. Depending on the receptivity of the female, this prodding lasts for a variable amount of time. The female may continue walking around for some time carrying the male, or, especially early in the process, the female may try to dislodge the male by pushing on him with the hind legs. Clasping of the female at the base of the metasoma by the male and continued walking by the female during this process were observed in *P. f. frigida* by Rau (1922) also.

Eventually the female opens the genital chamber by depressing the subgenital plate and partly extruding the sting. At this time the male immediately ceases prodding the female and fully extends the genitalia. The male then introduces his genitalia into the genital chamber of the female, except for the parameres which lie on either side of the apical tergum of the female. Once union of the genitalia has been accomplished, the male may release his hold on the female with the legs and mandibles and gradually fall over. During the actual process of mating the individuals remain motionless, except perhaps for a gradual and passive settling of the male

under the influence of gravity. Union varies somewhat in duration, but typically was seen to last about 15 seconds, which is the time noted for *P. f. frigida* by Shappirio (1948). In one case the female was still somewhat teneral and rather resistant to mating, and genital union lasted for about 150 seconds after three attempts to mount and an initial prodding by the male lasting about 180 seconds. Extrusion of the sting during copulation was also noted in *Smicromyrme rufipes* by Crèvecoeur (1930) and *Smicromyrme decora* (Smith) by Pagden (1934).

After copulation the male releases his genitalia and gradually withdraws them, the female sometimes starting to move restlessly just before this. The female then withdraws the sting and runs off. For some minutes after copulation the female often partly extends and withdraws the sting every few seconds. These pumping movements may possibly aid movement of the sperm into the spermatheca. The male grooms himself for a few seconds and then resumes his search for another female.

The attractiveness of a female to males diminishes rather rapidly after mating. In the laboratory, if a male contacted a female a few minutes after she had mated he would mount and attempt to mate as before, but after a few seconds to a few minutes he ceased prodding the female and left. A few hours after mating the female was even less attractive, and the male might mount but usually released the female immediately without even attempting to prod her metasoma. Females that had mated a day or more previously evoked no response from a male at all. In contrast, a male can copulate more than once, each time with a different female.

The attractiveness of an unmated female may be caused by some secretion which becomes masked or inactivated by a second secretion produced once mating has occurred. It is perhaps unlikely that the loss of attractiveness is merely the result of cessation of secretion after mating. One unmated female which died soon after emergence remained very attractive to males, evoking persistent prodding at the metasomal apex by the male even after she had been dead for more than a day. At that time the male maintained his hold on the dead female and continued his attempts at copulation for more than 40 minutes before they were separated.

The very short period of actual genital union in *P. f. frigida* is similar to that found in some other Sphaeropthalminae, such as *Dasymutilla* (Cottrell, 1936; Linsley *et al.*, 1955) and *Photopsis* (Ferguson, 1962; Salman, in Mickel, 1938), but contrasts with the situation in Mutillinae such as *Timulla* (Linsley, 1960; Sheldon, 1970) and *Smicromyrme* (Bertkau, 1884; Crèvecoeur, 1930; Pagden, 1934), and Rhopalomutillinae *(Rhopalomutilla)* (Bridwell, 1917; Pagden, 1938) in which copulation lasts for a long time (often in excess of an hour) and the male transports the female in flight, at least before actual genital union occurs and sometimes during copulation itself (Nonveiller, 1963).

Seasonal Cycle

During the investigations the numbers of *P. f. frigida* at each site increased and the proportion of active burrows of *L. zephyrum* decreased as the season progressed. At the two sites with the largest numbers of mutillids, the bee colonies had been practically exterminated by the end of the season. At this time many cocoons of *P. f. frigida* and *Myrmosula parvula* were found when digging, but immature bees were rare. The impression was obtained that the virtual elimination of the bee colonies could be attributed to the mutillids and the myrmosids. The proportion of mutillids to myrmosids varied amongst the sites; mutillids were most ef-

fective at one stream bank site, whereas myrmosids were predominant at the Wakarusa site. Similar extermination of an aggregation of *Lasioglossum versatum*, apparently by *P. f. frigida*, was observed by Michener (1966).

P. f. frigida overwinters in the prepupal stage (see also Batra, 1965). The exact stimulus which causes diapause in the prepupae at the end of the season is not known, but it is probably lowered temperature. In areas such as Kansas where the active season lasts some five months or longer there is a number of generations, probably at least three, during this period. Developing pupae were found in the field at the end of September; these undoubtedly produced the last generation of adults. Krombein (1963) also found *P. f. frigida* to be multivoltine in Maryland. In Ontario, where the season of activity is much shorter, *P. f. frigida* is univoltine (Knerer and Atwood, 1967). *Sphaeropthalma (Photopsis) unicolor* (Cresson), which occurs in western North America from Washington to Baja California, also shows a range of one generation per year in the north to four to six in the south (Ferguson, 1962). In areas where no season is entirely unfavorable for development there is probably an indefinite number of generations per year without any period of diapause. This is the case in *Chrestomutilla glossinae* in Rhodesia, although the developmental period is much longer during the winter than in the summer (Heaversedge, 1970).

Although Mutillidae usually overwinter as prepupae, this is not invariably the case since Potts and Smith (1944) found *Dasymutilla aureola pacifica* (Cresson) hibernating as adults in Alameda County, California, and Evans and Miller (1969) observed overwintering of marked adults of *Dasymutilla nigripes* (Fabricius) in Michigan.

Host Spectrum

P. f. frigida parasitizes a number of species of bees, all members of the subfamily Halictinae (Halictidae), as well as a wasp in the family Eumenidae (Vespoidea). *P. f. frigida* (Smith) has been reared from the cells of *Lasioglossum (Dialictus) zephyrum* (Smith) (Batra, 1965, 1966), *L. (Dialictus) versatum* (Robertson) (Michener, 1966), and *L. (Evylaeus) cinctipes* (Provancher) (Knerer and Atwood, 1967), all of which nest in the soil, and also from *L. (Dialictus) coeruleum* (Robertson) (Barrows, pers. comm.), which nests in rotting logs. *P. f. frigida* has been reared also from cells which were probably those of *L. (Dialictus) imitatum* (Smith) (Brothers and Michener, pers. obs.). Females of this mutillid have also been seen entering the nests or have been found in the burrows of *L. imitatum*, *L. (Dialictus) rohweri* (Ellis) and *Augochlorella striata* (Provancher) (Michener and Wille, 1961) and *L. (Dialictus) laevissimum* (Smith) in Kansas (Michener, pers. comm.). The records of invasion of nests of *"Halictus (Chloralictus) pruinosus"* by Melander and Brues (1903) probably refer to *L. zephyrum* (Michener, pers. comm.). Quite probably *P. f. frigida* will be found to be parasitic on additional species of Halictinae which nest in suitable areas, since it is widely distributed in Canada and the United States east of the Rocky Mountains (Krombein, 1951b). Similarly, *Mutilla europaea*, which is also a very widely distributed species, is parasitic on numerous species of *Bombus* in Europe and Asia (Mickel, 1928; Miyamoto, 1959, 1963; Taniguchi, 1955).

There is also a record of *P. f. frigida* being reared from a multicellular mud nest of the eumenid wasp, *Ancistrocerus birenimaculatus* (Saussure), in Georgia (Fattig, 1943). The problems involved in gaining access to the young of such a wasp

are quite different from those involved in attacking halictine bees, since the mutillid must penetrate the wall of a hard, exposed mud nest, and then also penetrate the host cocoon. This record should thus probably be considered doubtful until it can be confirmed by additional rearings.

A lack of host specificity is, however, not unusual for the Mutillidae: *Stenomutilla argentata* (Villers) has apparently been found parasitic on Eumenidae (Vespoidea), Megachilidae (Apoidea), and Clythrinae (Chrysomelidae, Coleoptera) (Giner Marí, 1944), a more heterogeneous range of hosts than is suspected for *P. f. frigida*.

Descriptions of Immatures

Egg (Fig. 11)

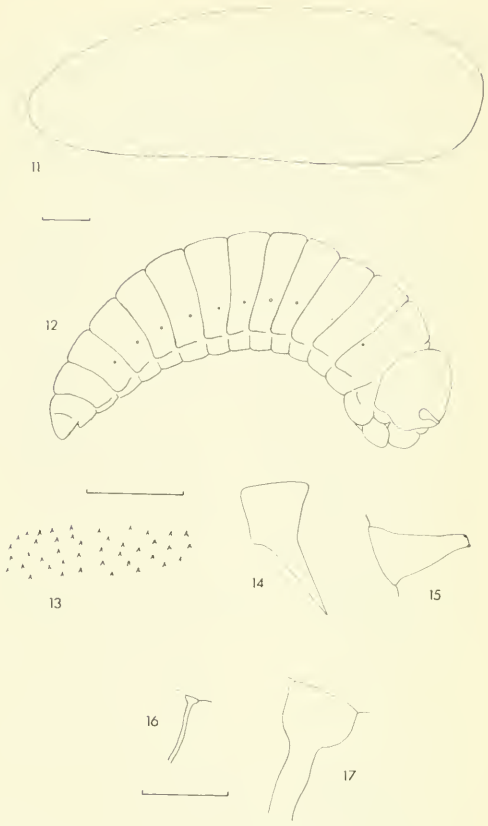
Length 0.79-0.94 mm, width 0.24-0.30 mm; slightly arcuate and weakly tapered caudally. Chorion 5 μ thick, smooth, without any ornamentation.

The egg is relatively thicker than that of *Dasymutilla bioculata* (Fig. 41; Cottrell, 1936), *Sphaeropthalma (Photopsis) orestes* (Fox) (Ferguson, 1962), *Stenomutilla argentata* (Ferton, 1921), *Ronisia barbara brutia* (Petagna) and *Mutilla europaea* (Andre, 1899-1903). It further differs, from that of *S. orestes* at least, in the absence of any sculpturing.

Larval Instars

The larvae are of the typical aculeate type, with an almost colorless head capsule, thirteen postcephalic segments, and lacking appendages.

First instar (shortly after hatching; Figs. 12-18): length 0.98 mm, maximum width 0.28 mm; elongate, body approximately cylindrical anteriorly, tapering posteriorly from about the tenth postcephalic segment; pleural and dorsal lobes absent; anus subterminal, ventral, slitlike. Ten pairs of simple spiracles, the second tho-



Figs. 11-17. Egg and first instar larva of *Pseudomethoca f. frigida*. **11,** egg; **12,** larva, lateral view; **13,** dorso-lateral spinules of larva; **14,** mandible; **15,** antenna; **16,** second thoracic spiracle; **17,** first abdominal spiracle. Scales: 11-12=0.1 mm; 13-15=0.05 mm; 16-17=0.005 mm.

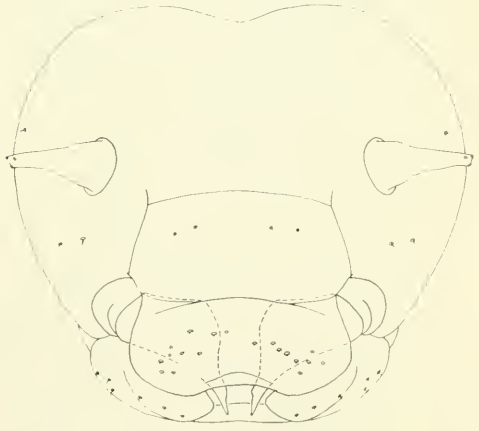
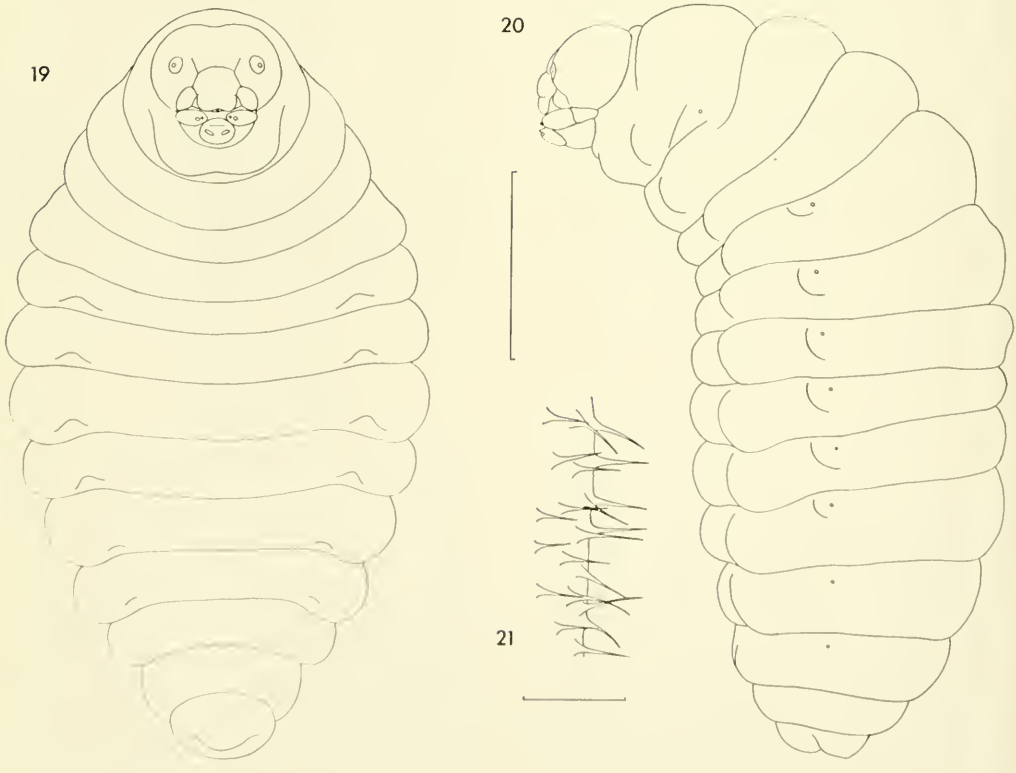


Fig. 18. Head of first instar larva of *Pseudomethoca f. frigida*, anterior view. Scale=0.1 mm.

racic pair much smaller than the others and possibly nonfunctional; atrium of functional spiracles hardly differentiated, no distinct subatrium. Integument smooth ventrally, otherwise clothed with minute spinules and a very few tiny setae.

Head 0.24 mm wide, 0.09 mm high (exclusive of labrum and mouthparts), unpigmented except for apices of mandibles, with very few minute, scattered setae. Vertex weakly depressed medially, without parietal bands. Antennal orbits approximately circular, about 35 μ in diameter; antennal papillae large, 56 μ long with three sensilla apically. Clypeus with four setae and no pores. Labrum 114 μ wide, 44 μ in median height, with a fairly strong median emargination; surface with sensilla as figured. Epipharynx apparently smooth. Mandible 1.6 times as long as basal width, without setae or irregularities; apex simple with a very faint protuberance preapically within, suggesting a blunt tooth. Maxilla apparently smooth, with a few setae; palpus and galea apparently undeveloped. Labium apparently smooth, without palpi.

Diapausing fifth instar (Figs. 19-32): length 4.0 mm, maximum width (third abdominal segment) 2.4 mm; compact fusiform to onisciform, more gradually tapering anteriorly than posteriorly, anterior extremity deflexed ventrally; pleural lobes (ventrolateral tubercles) present on second and third thoracic and first eight abdominal segments, rounded; indistinct dorsal lobes present on the same segments; anus terminal, slitlike. Ten pairs of small, circular, scarcely pigmented spiracles, the second thoracic spiracles less than half the



FIGS. 19-21. Diapausing fifth instar larva of *Pseudomethoca f. frigida*. **19**, ventral view; **20**, lateral view; **21**, dorso-lateral spines. Scales: 19-20=1.0 mm; 21=0.05 mm.

diameter of the others and without differentiated atrium or subatrium; other spiracles with broad peritreme, atrium with fine simple transverse ridges, simple unarmed primary tracheal opening, and subatrium. Integument smooth ventrally with a few sensory setae, dorsally and laterally covered with fine, dense spines and a few setae, each about 20 μ long, the latter denser on the tubercles; tenth abdominal segment smooth except for a few minute spinules anteriorly in irregular short transverse dorso-lateral rows.

Head 0.68 mm wide, 0.47 mm high (exclusive of labrum and mouthparts); unpigmented except for tentorium, hypostomal thickenings, antennal papillae, apical halves of mandibles, maxillary cardines and stipites (very weakly pigmented), palpi and galeae; with a few scattered setae. Vertex weakly depressed medially; parietal bands absent. Antennal orbits circular, very large, about 100 μ in diameter; central papilla weakly developed, flattened, with three sensilla. Clypeus with four setae and two pores. Labrum 230 μ wide, 80 μ in median height, with a fairly strong median emargination; anterior margin with many spinules; surface with sensory cones, setae and sensilla as figured. Epipharynx with a median patch of sensory pores, with spinules mostly arranged in irregular rows antero-laterally. Mandible about twice as long as basal width, without setae or irregularities, with four apical teeth, basal tooth smallest and entire or divided into denticles apically, often differing on the two sides of the same speci-

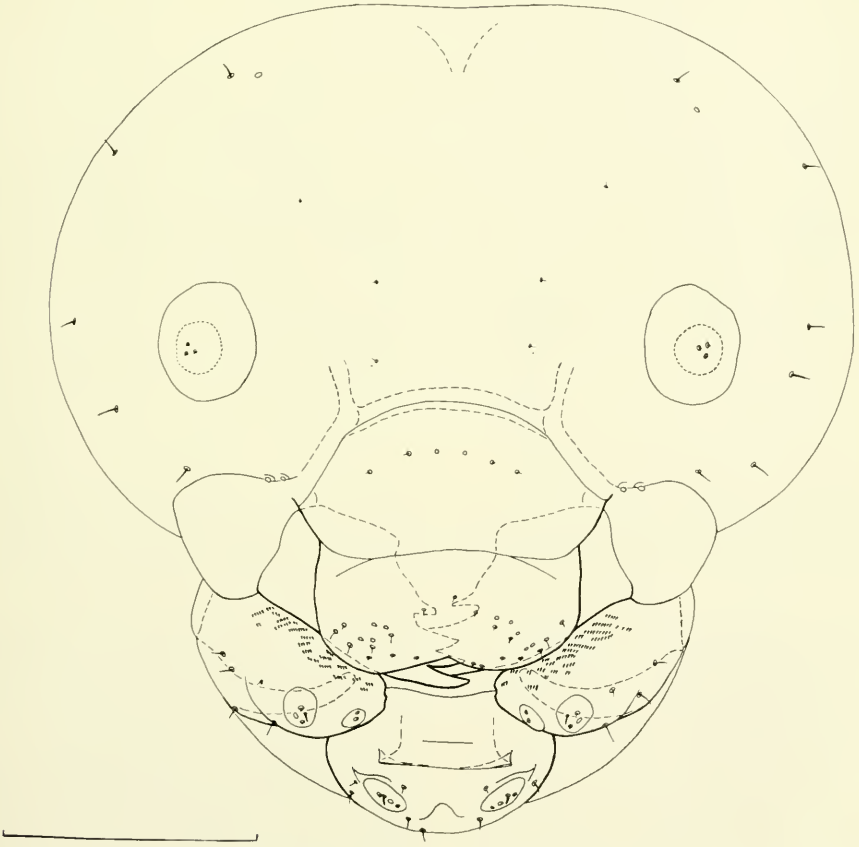
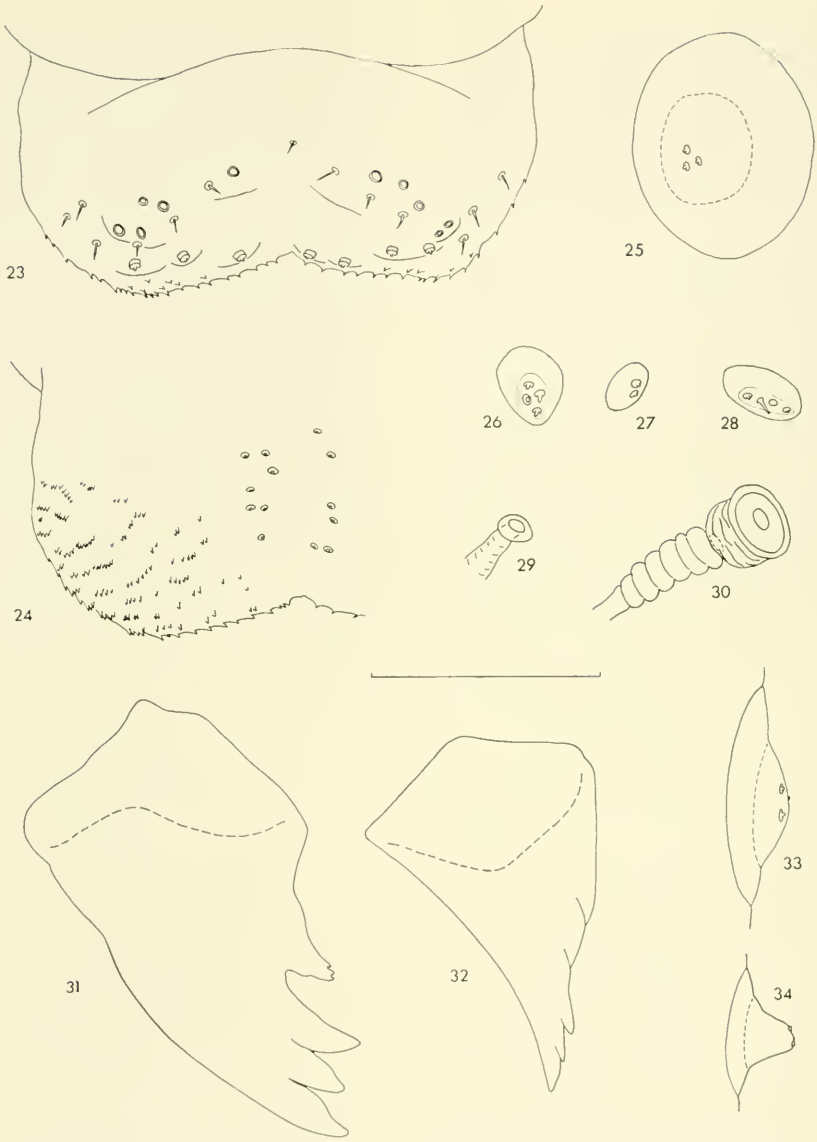


Fig. 22. Head of fifth instar larva of *Pseudomethoca f. frigida,* anterior view. Scale=0.2 mm.



FIGS. 23-34. Fifth instar (23-31, 33) and fourth instar (32, 34) larvae of *Pseudomethoca f. frigida*. **23**, labrum; **24**, epipharynx; **25**, antenna, surface view; **26**, maxillary palpus; **27**, galea; **28**, labial palpus; **29**, second thoracic spiracle; **30**, first abdominal spiracle; **31**, mandible; **32**, mandible; **33**, antenna, profile; **34**, antenna, profile. Scale=0.1 mm.

men. Maxilla with spinules dorsally similar to those on epipharynx, with a few lateral setae; palpus about 13 μ long, 30 μ wide at the base, with four sensilla apically; galea about 6 μ long, about 10 μ wide basally, with two sensilla. Labium with prementum about 1.8 times as broad as high, with a few apical setae, smooth oral surface, and without spines or papillae; labial palpi about twice as broad as long, with four apical sensilla; spinneret broad, acutely protuberant at each side.

Non-diapausing, defecated fifth instar: length almost three times maximum width (e.g., 5.8 × 2.1 mm, 4.3 × 1.3 mm, for large and small individuals); elongate-

fusiform, slightly contracted behind fourth postcephalic segment, more gradually tapering posteriorly than anteriorly; rounded pleural lobes and small median dorsal lobes present on second to tenth postcephalic segments. Otherwise as for diapausing larva.

Variation between larval instars: Apart from a general increase in body size at each molt (Fig. 9), the most marked changes occur at the molt from the third to fourth instar. In the first three instars the antennae are elongate, the mandibles are essentially simple and the spiracles have the atria hardly differentiated. The fourth instar has the antennae much shorter (Fig. 34), the mandibles with three weak teeth (Fig. 33) and the spiracles with well-differentiated atria and subatria. The change from second to third instar is evident only in the shorter antennae of the third instar larva. The first and second instars are virtually indistinguishable except by measurement of the head capsule.

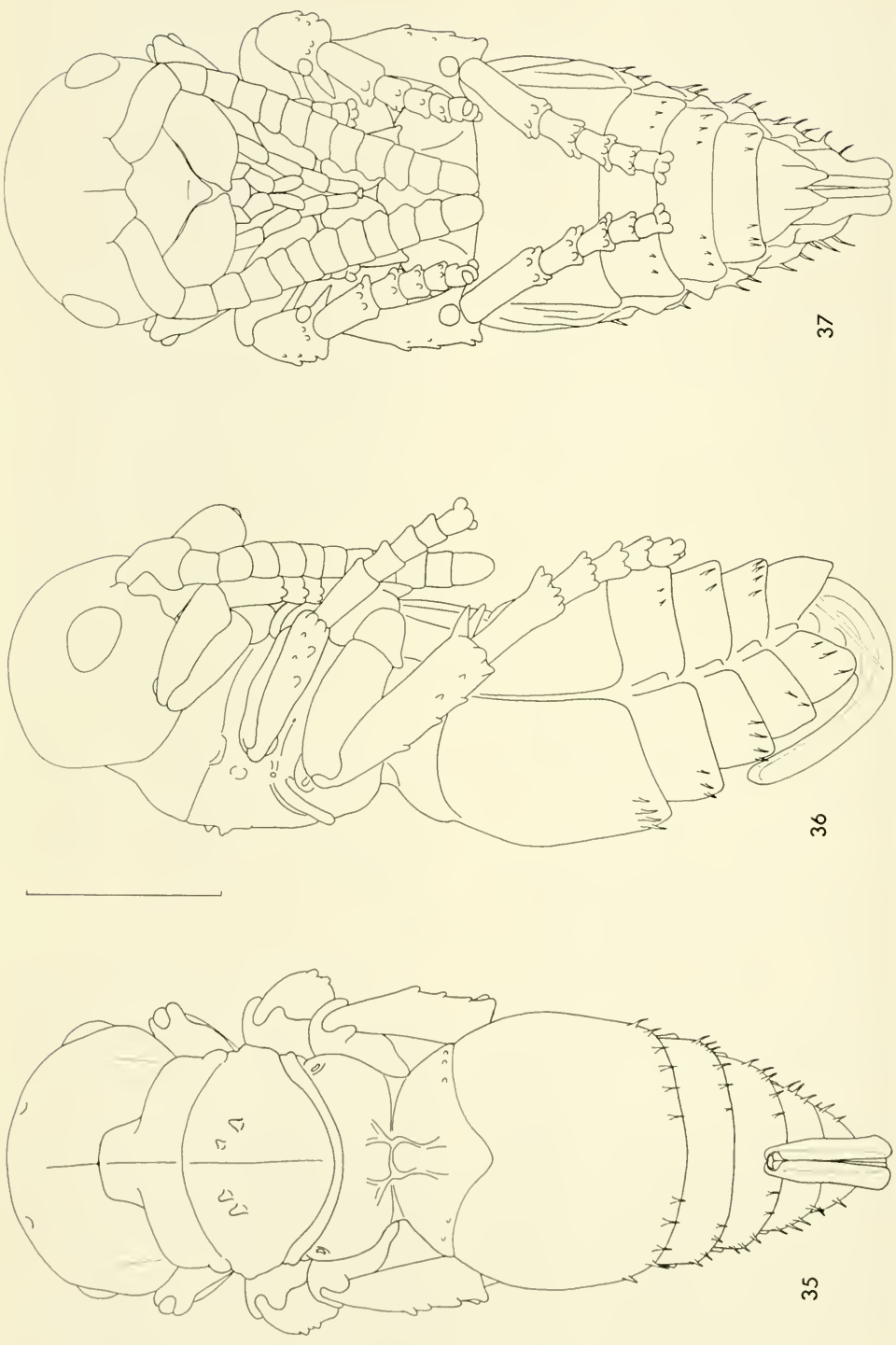
Similar changes, at least in the antennae, apparently occur in *Sphaeropthalma (Photopsis)* spp. (Ferguson, 1962) and *Stenomutilla argentata* (Ferton, 1921).

The only other mutillid for which the mature larva has been described in any detail is *Smicromyrme rufipes* (Mutillinae) (Maréchal, 1930; Grandi, 1961:397). This species shows many similarities to *P. f. frigida*. Apparently it also has the second thoracic spiracles reduced, this being definitely stated by Maréchal, although Evans (1965) interpreted Grandi's figure as showing all the spiracles of equal size. (Grandi does not mention the spiracles in his description.) The mature larvae of *Sphaeropthalma (S.) pennsylvanica scaeva* (Blake) and *"Ephuta" aequatorialis* André (Sphaeropthalminae) are also similar, with reduced second thoracic spiracles and quadridentate mandibles. The mature larva of *Stenomutilla freyi* (Brancsik) also has quadridentate mandibles, but Seyrig's (1936) figure shows ten pairs of similar spiracles. Janvier (1933) gave short descriptions and inadequate figures of the larvae of *Dimorphomutilla lunulata* and *Neomutilla attenuata* and a species of *"Photopsis"*. They appear to be similar to that of *P. f. frigida* in general form at least, although Janvier apparently found differences in the form of the mandibles and the number of spiracles. Lloyd (1916) found that there are apparently 11 pairs of spiracles in the larva of *Chrestomutilla glossinae,* and that the mandibles are quadridentate, but he misinterpreted the morphology of the cephalic appendages.

The larvae of the Mutillidae are very similar to those of the Tiphiidae, and are not as readily separable from them as was indicated by Evans (1965). There seem to be no characters by which the larvae of these two families can readily be distinguished. The larvae of *Myrmosula parvula* (Tiphiidae; Myrmosinae) are also very similar to those of Mutillidae (Brothers, in prep.). The larvae of Mutillidae and Tiphiidae key out with the Vespidae, Scoliidae, Pompilidae, Formicidae, Chrysididae, etc. in the key to the larvae of Hymenoptera provided by Michener (1953).

Pupae

The pupae exhibit essentially the shape and form of the adults, the females lacking wings and ocelli and with the sting sheaths exserted, and the males possessing wings, ocelli and rudimentary genitalia. The main features peculiar to the pupae are various tubercles and spines. Despite Michener's (1954) suggestion that in bees these may have originated to provide space for the development of hairs, this does not seem to be their function in *P. f. frigida*. The projections may serve to prevent adhesion to the cocoon should it become damp inside. This is perhaps sup-



FIGS. 35-37. Pupa of *Pseudomethoca f. frigida*, ♀. **35**, dorsal view; **36**, lateral view; **37**, ventral view. Scale=1.0 mm.

ported by the fact that many Hymenoptera with relatively hairless adults (e.g., at least some pompilids and sphecids), have pupae with extensive development of spines (see Williams, 1919:91, 129).

Female (Figs. 35-37): Head with sac-like, apically papillate mandibles; twelve-segmented antennae with indistinct segmentation, weakly tuberculate. Mesosoma dorsally with pro-meso, meso-meta and metathoracic-propodeal sutures visible; about four mesoscutal tubercles and a pair of lateral mesothoracic tubercles; propodeum with two longitudinal ridges; mid and hind coxae and trochanters with blunt apical teeth; mid and hind tibiae each with two rows of tubercles externally, a few tubercles apically and a large pair of spines enclosing the apical spurs. Metasoma with two longitudinal ridges and a few small preapical tubercles on first tergum; a variable number (up to 12) of small preapical spines on second to sixth terga and a smaller number of spines preapically on third to fifth sterna; last sternum bilobed; sting exserted, curved dorsally, extending anteriorly to the middle of fourth tergum, comprised of five stylets.

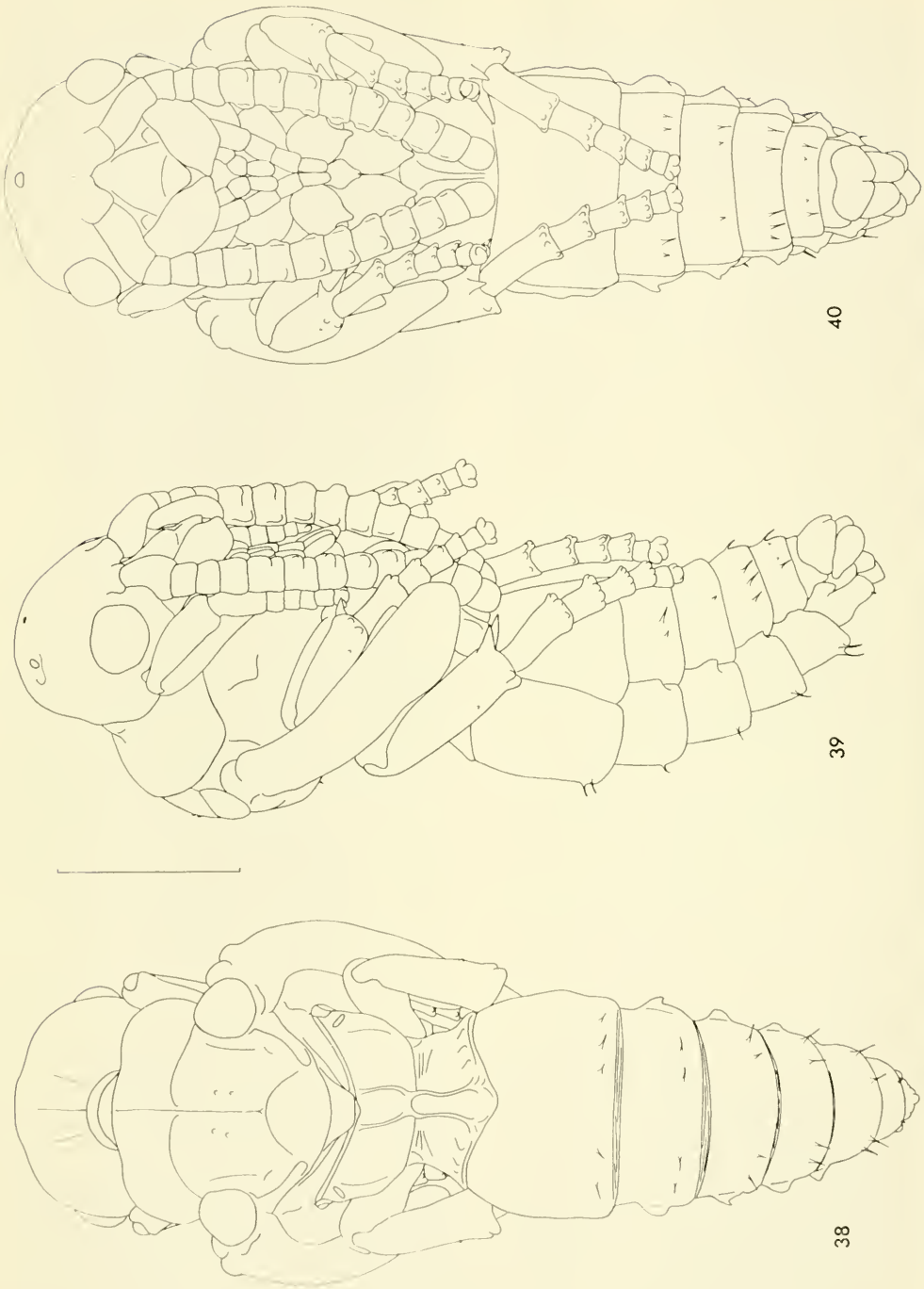
Male (Figs. 38-40): Head with sac-like, apically papillate mandibles; thirteen-segmented antennae with indistinct segmentation, tuberculate on fifth to twelfth segments. Mesosoma with distinct sutures, about four small mesoscutal tubercles; propodeum with two longitudinal ridges; mid and hind coxae with blunt teeth apically; mid and hind tibiae each with one minute preapical tubercle externally, a few tubercles apically in addition to the pair enclosing the tibial spurs. Metasoma with two longitudinal ridges on first tergum; a variable number (up to about eight) of small preapical spines on second to seventh terga and a smaller number of smaller spines preapically on third to sixth sterna; apex with three pairs of lobes ventrally, a single lobe dorsally.

The pupae of *P. f. frigida* are rather similar to those of *Dasymutilla bioculata* (Cottrell, 1936) and *Sphaeropthalma (Photopsis) blakeii* (Fox) (Ferguson, 1962), but are less spinose than those of *Smicromyrme rufipes,* especially along the lateral margins of the metasoma (Maréchal, 1930). In some tiphiid pupae such as *Methocha striatella* Williams (Methochinae), the sting is exserted and similar to that in Mutillidae (Williams, 1919:72). However, the sting is very short in the female pupa of *Myrmosula parvula* (Myrmosinae), the metasomal apex superficially appearing not much different from that in the male pupa (Brothers, in prep.).

OBSERVATIONS ON *DASYMUTILLA BIOCULATA* (CRESSON) BY COTTRELL (1936)

Apart from my study on *Pseudomethoca f. frigida* and the work of Ferguson (1962) on species of *Sphaeropthalma (Photopsis),* the only reasonably complete study of the life history of a North American mutillid is that on *Dasymutilla bioculata* in Minnesota by Cottrell (1936). Since Cottrell's study has not been published, a rather complete summary of his and related work is presented herein.

Cottrell's observations were made in a sand dune region one mile east of Fridley, Anoka County, Minnesota (see Mickel, 1923), where *D. bioculata* is parasitic on at least two species of bembicine wasp (Sphecidae), *Bembix pruinosa* Fox and *Microbembex monodonta* (Say). Individuals which develop on the former, larger species are larger than those which develop on the smaller *M. monodonta* (Mickel, 1924). [The biologies of the two host species are described by Evans (1957, 1966).] At suitable temperatures, the female mutillids run on the sand, burrowing at intervals, and the males fly close to the surface in search of females. When



FIGS. 38-40. Pupa of *Pseudomethoca f. frigida*, ♂. **38**, dorsal view; **39**, lateral view; **40**, ventral view. Scale=1.0 mm.

the temperature reaches 50° C the females dig deep into the sand or climb the vegetation to escape the heat. Chapman *et al.* (1926) found that the extreme range of temperature over which *Dasymutilla* spp. were active in the Fridley area was about 18° to 45° C (substrate sand temperature). Since the sand temperature often exceeds

this at midday, the mutillids tend to be active in the morning and especially the late afternoon. This pattern was confirmed by Nonveiller (1963), who found that most mutillid activity in Crete occurred within the temperature range of approximately 25° or 30° to 40° C.

Cottrell made laboratory observations by placing bembicine cocoons in artificial burrows in moist sand in a glass-sided observation chamber. Newly emerged female mutillids were then introduced. From emergence to the first oviposition females merely burrowed in the sand and fed from cotton soaked in sugar water. The mutillids first showed interest in the cocoons about a month after emergence, probably indicating that development of the oocytes may take a long time. The time involved may have been unnaturally long due to the artificial conditions, especially with regard to feeding. In other species, the females often have a complement of ripe oocytes at emergence (Ferguson, 1962; Heaversedge, 1969b). Some females of *D. bioculata* would oviposit only in the dark, i.e., if the cocoon was covered with a blackened microscope slide.

When a female is ready to oviposit, she examines the host cocoon carefully. The mutillid seems to seek a weak spot in the cocoon wall, and works some of the sand grains composing the wall loose with the mandibles. Considerable force is exerted by the female and the body is bent dorsally so that the mesosoma is pressed against the wall of the burrow to provide extra leverage. When a small area is cleared of sand the wasp bites through the membranous wall of the cocoon. The opening is rounded by inserting the mandibles and twisting the head. The female then positions the tip of the metasoma over the opening and exserts the sting. If the opening is not large enough it is enlarged. During oviposition the sting is introduced into the cocoon, but it does not touch the host larva or pupa. Sometimes, if the opening is small, the egg is forcibly pushed into the opening after much manipulation. The egg is elastic and may be deformed during laying. The female can apparently detect a cocoon that has already been parasitized, since none could be induced to oviposit in such cocoons. This contrasts with the situation in *Chrestomutilla glossinae* in which superparasitism is the rule (Heaversedge, 1969b), although the mechanism by which this occurs is not known and it may be that the female lays more than one egg at a time in each puparium. The maximum number of eggs laid by a single female of *D. bioculata* was ten, yet some individuals laid only one or two even if supplied with unlimited host cocoons, possibly because of inadequate supplies of nutrients under artificial conditions. As soon as the egg has been laid, the female seals the opening in the host cocoon by gathering sand grains from the sides of the burrow in the mandibles and cementing the grains to the sides of the opening by means of a salivary secretion. The hole is gradually built shut, a process that may take 30 minutes. The sealed area is not as tough as the original cocoon wall. Lamborn (1915) noted that the female of *Chrestomutilla glossinae* sealed the oviposition opening in the puparium of *Glossina* by means of a salivary secretion. The oviposition aperture in the cocoon of *Trypargilum politum* (Say) is similarly sealed by *Sphaeropthalma (S.) pennsylvanica scaeva* (Brothers, pers. obs.).

In *D. bioculata* the oviposition opening is almost invariably made in the anterior half of the cocoon. Probably the position of the oviposition aperture is such that the egg is usually deposited on the venter of the host larva (Fig. 41) in an anterior position and in the concavity formed by flexure of the anterior end of the larva, a position always assumed by the prepupa of the host. A female never penetrates a

FIGS. 41-42. Egg and larva of *Dasymutilla bioculata* (from Cottrell, 1936). **41,** egg on prepupa of *Bembix pruinosa;* **42,** first instar larva on prepupa of *Bembix pruinosa.*

cocoon before the host has defecated. The fecal material that seeps through the cocoon wall is perhaps necessary for proper positioning of the oviposition opening. The presence of this external cue to the suitability of a cocoon for parasitization may eliminate the necessity for probing of the host by the sting such as occurs in *P. f. frigida.*

The *D. bioculata* egg hatches after about three days, the chorion being split at the anterior end. The first instar larva (Fig. 42) is about 2 mm long, with head, three thoracic and nine abdominal segments, and with six pairs of spiracles, a pair on segments four to nine inclusive. The observed number of segments as well as the number of spiracles differs from that in *P. f. frigida,* which has 13 postcephalic segments and 10 pairs of spiracles. Since the spiracles are minute, Cottrell may have missed some of them. Once free of the chorion, the larva crawls around on the host and locates a suitable place to pierce the host cuticle, usually at a point between body segments ventrally. The larva feeds

on the exuding juices. It moves around prior to each molt or if disturbed. The entire host except for the cuticle is consumed, the integument being pushed to the posterior end of the host cocoon when the mutillid larva is about to spin its cocoon. This contrasts with *P. f. frigida,* in which the larva consumes the entire host, including the cuticle. If the *D. bioculata* larva was supplied with additional host larvae it consumed these also, even to the point where it became so distended that it could not spin a cocoon. There are four larval instars, with durations as follows: first instar about five days, second instar about three days, third instar about one day, fourth instar to start of spinning about one day. There are five larval instars in *P. f. frigida.* Cottrell's "first" instar in *D. bioculata* may actually include the second also.

Fully fed larvae of *D. bioculata* usually lie quiescent for about two days before spinning. At the start of spinning the larva examines the inside of the host cocoon and then lays down threads indiscriminately on it. As the number of threads increases, the larva reverses position, working at alternate ends of the cocoon. The spinnerets consist of two small openings, one on either side of and below a central opening in the labium. This impression may also be given by a transverse slit with protuberant lips laterally, which could produce two strands of silk, as in *P. f. frigida.* The cocoon of *D. bioculata* is lined on the inside with a gelatinous substance. Spinning takes about two days. The overwintering prepupal stage begins in August and usually ends the following late June or July, when pupation occurs.

During pupation the anterior segment collapses and a constriction forms behind the fourth segment dorsally. The cuticle and the lateral tubercles become shriveled. The fat body becomes concentrated in the anterior part of the metasoma. This probably represents accumulated uric acid in urate cells (see Wigglesworth, 1965). At 32° C the pupal stage lasted 10 to 12 days. The pattern of development of coloration in a female was as follows: about 40 hours after pupation the eyes began to color; the wing scars started to darken after another 100 hours, the mesosoma gradually coloring; after a further 170 hours the whole insect was a definite orange color; 100 hours later pubescence was visible and color differentiation occurred, the legs, antennae and parts of the metasoma becoming black; emergence took place about 70 hours later. A total of 480 hours, an unusually long time, was thus required for pupal development in this instance.

Molting from the pupa occurs after the cuticle becomes wrinkled and stretched tightly across the anterior part of the body so that it splits across the back of the head. The cuticle is then worked to the rear of the body. After molting the adult remains quiescent for one or two days inside the cocoon during which time hardening takes place. After this period the adult escapes by cutting through the anterior end of the cocoon with the mandibles and pushing out the operculum-like lid so formed. Similar cutting of a cap from the end of the host cocoon occurs in *Sphaeropthalma (S.) pennsylvanica scaeva* (Brothers, pers. obs.). The males emerge five to ten days before the females. In nature the males live one to two weeks and the females about a month.

D. bioculata may not always be univoltine, since some larvae did not pupate when subjected to low temperatures, but emerged the second year after the egg was laid. About half of the larvae of a batch which overwintered at a temperature of no less than 10° C pupated and emerged at the normal time the following summer, although they had not been subjected to low temperatures. A sample of those that

had not pupated were subjected to low temperatures (successively from 30° to —19° C and back), with some others being used as controls (kept at room temperature). In this case the experimental larvae pupated but the controls did not. Thus, pupation in some larvae is dependent on exposure to low temperatures, but in others is not. Ferguson (1962) found in *Sphaeropthalma (Photopsis) blakeii* that pupation could be induced by a rapid increase in temperature to 31° C, or by a cumulative effect if pupae were kept at a relatively high temperature (20° C) throughout. A specimen of *Sphaeropthalma (S.) pennsylvanica scaeva* which overwintered in the laboratory at approximately 20° C also emerged early the following spring without cold treatment (Gordh, pers. comm.).

Mating of *D. bioculata* takes place almost immediately after adult emergence. The male makes advances toward the female, vibrating the wings, until he grasps her tightly with the legs. The male does not hold the female with the mandibles. During mating the tip of the metasoma of the male is curved ventrally over that of the female, and the metasoma of the female is tipped up slightly. Copulation lasts about 20 seconds. Virgin females mate without any resistance, but once mated a female resists further attempts. A male is apparently aware if a female has already mated since he does not persist in attempts to mate with such a female. A female will not oviposit before mating, even if she has mature oocytes.

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A FIELD STUDY OF COSTA RICAN LIZARDS

By
HENRY S. FITCH

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A Field Study of Costa Rican Lizards

Henry S. Fitch

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A Field Study of Costa Rican Lizards

Henry S. Fitch[1]

ABSTRACT

From October 1967 to March 1970 local populations of 26 species of lizards including gekkonids, iguanids, anguids, teiids, and scincids, were studied at 15 localities on 23 study areas in Costa Rica. Capture-mark-recapture procedures were used and the field records were supplemented by examinations of museum specimens. More than 17,000 field records were accumulated, representing tropical and subtropical rain forest, xeric lowland forest, gallery forest along streams, ocean beach, and various transitional situations. The species studied were a spectrum of ecological types; some were euryecic and showed significant ecological change from one study area to another with different habitat or climate. Preferred body temperatures ranged from 19.5°C in *Anolis tropidolepis* to approximately 40°C in *Cnemidophorus deppii*. Heliothermic species were found to have the highest body temperatures, *Ctenosaura similis* and *Ameiva undulata* maintaining levels only a little below that of *Cnemidophorus deppii*, and a little higher than the species of *Sceloporus*. In basilisks, skinks and most kinds of anoles, preferred body temperatures were found to be between 27 and 35.5°C.

Growth to breeding maturity occurred in 4 to 8 months in most kinds of small lizards, but the largest kinds required a longer time—at least a year in *Basiliscus basiliscus* and 2 years or more in *Ctenosaura* and *Iguana*. In most species marked individuals that were recaptured after intervals of a month or more had moved no more than 15 m, and typical home ranges of most species were judged to have radii in the range of 5 to 12 m. Reproductive cycles were found to be closely correlated with climate. In northwestern Costa Rica where there is little precipitation from December to April, most species including *Anolis cupreus, A. sericeus, A. intermedius, Ctenosaura similis, Ameiva undulata, Sceloporus variabilis* and *Cnemidophorus deppii* cease to produce eggs in the dry season. In the warm, humid climate of the Caribbean lowlands there is year-round reproduction in most species but its level changes throughout the annual cycle, with more egg-laying in the wetter months and less in the drier months. In *Basiliscus vittatus* and *Scincella cherriei* changes in the level of reproduction are most prominent; in *Anolis humilis* at San Miguel de Sarapiquí and *Gonatodes albogularis* at Limón there is relatively little change in the level of reproduction throughout the year. Most nearly uniform year-round reproduction occurs in *Anolis tropidolepis* in montane cloud forest in a climate that is cool and moist throughout the year.

INTRODUCTION

The present study was conceived in 1964, as an intensive and protracted investigation on a series of tropical reptile populations, with attention focused on reproductive cycles and the roles of various climatic factors in controlling them. Preliminary field work was done at many of the study areas in early 1965, but the main field effort was made during a continuous eight-month period in 1967-1968 with four shorter sojourns of one to two months each in late 1968 and 1969, and early 1970.

At the time of the study's inception relatively little had been published regarding the reproductive cycles of tropical reptiles but in the ensuing eight-year period much interest in the subject has developed, and many investigations have been under-

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taken, some on the same species and even at the same localities involved in my own field work. These studies have generally concentrated on single species, often at a single locality. Much information is now available regarding the reproductive cycles of tropical reptiles, and some of the kinds herein discussed have already been studied. However, the present study was of longer duration than most, and comparative data were gathered for many species simultaneously. For some euryecic species, studied at two or more localities under different climatic conditions, there was especially favorable opportunity to assess the significance of temperature and moisture in the timing of events associated with reproduction. Although determining the effects of climatic factors on reproductive cycles was the prime objective, other interrelated aspects of the ecology were included in the study. Population structure was considered a key to understanding reproductive cycles, and population dynamics were investigated in each common species. Study of growth, by capture, marking, and recapture, constituted a major part of the total effort, as it was considered essential to an understanding of the annual cycle in each species.

Any kind of lizard that could be found in adequate numbers at a reasonably accessible locality was studied, but effort was made to include types representing diverse sizes, trophic levels, habitats, climates and phylogenetic groupings. The study was field oriented, and undertook to analyze natural populations without altering them. Procedure ordinarily did not involve removal of individuals, which were only momentarily restrained at the time of capture. The need for information regarding state of the gonads necessitated sacrifice of some animals, but their numbers were relatively small; ordinarily they were taken outside (but adjacent to) the areas that contained marked populations.

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METHODS AND MATERIALS

For sampling, 15 localities were selected distributed across Costa Rica from east to west and from north to south (Fig. 1). At some of the localities there were two or more study areas, depending on the local distribution and abundance of the species studied. Sampling ordinarily consisted of capturing the common species alive in large numbers, and processing each individual by measuring it, determining its sex and breeding status, and marking it for future recognition. Measurements were taken by pressing the animal against a ruler and reading to the nearest millimeter the snout-vent length, and tail

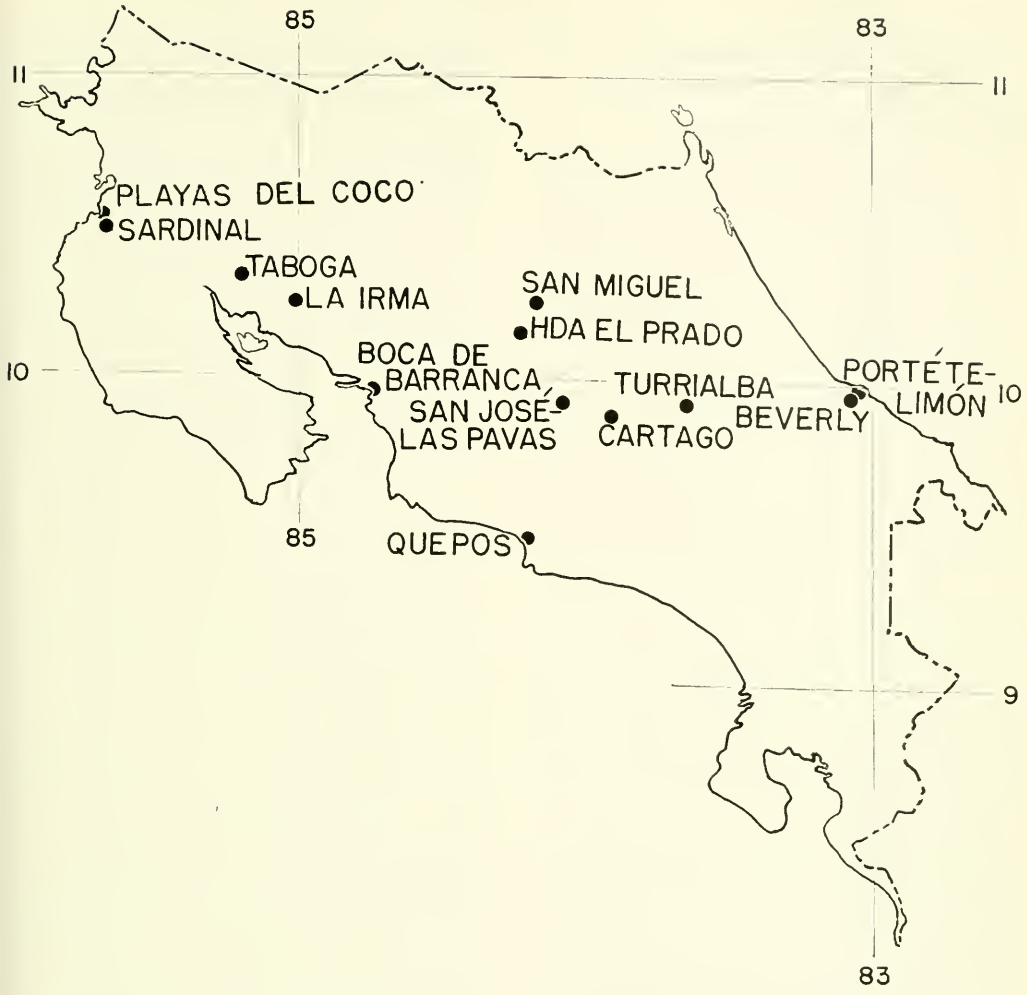

Fig. 1. Map of Costa Rica showing the 15 localities where population studies of lizards were made.

length with the original and regenerated parts recorded separately. Weights were recorded during the latter part of the study only, and were measured to the nearest tenth of a gram with Oskar Ludi spring scales. Reproductive condition of females was judged from their external appearance —whether collapsed and wrinkled from recent egg-laying, or of normal nongravid conformation, or slightly, moderately, or greatly distended with eggs or embryos. In some of the larger species, manual palpation confirmed the presence of unlaid eggs and provided information about the size and number of eggs in the clutch.

Lizards were marked chiefly by cutting off toes at approximately midlength. At least two toes were clipped on each lizard, always on different feet. In species that were processed in large numbers it became necessary to clip toes on three and eventually all four feet. Toe-clipping involved temporary laming and some permanent handicapping, especially in the scansorial and cursorial species, but alternatives such as branding, banding or tagging were judged to be even less satisfactory. Normally each lizard, besides being toe-clipped, was marked with a dab of paint before release. The color and position of

the mark occasionally served for individual recognition, but more frequently served to distinguish the recently processed lizards from others in the population.

In some of the populations studied, the lizards were so wary that capturing enough of them for an adequate sample would have consumed an inordinate amount of time. Also it would have resulted in bias, because the smaller and younger individuals are in some instances more readily caught than the larger and older. As a compromise lengths were estimated to the nearest millimeter in those seen at close range. Frequent checks, when the same individual was first estimated and then actually measured, showed that the percentage of error in the estimates was small after the observer had acquired sufficient experience.

Techniques for capturing lizards uninjured varied greatly according to the species and the situation. Anoles were usually caught by hand either on the ground or on vegetation. Effectiveness of stalking and securing the quarry with a rapid grab was tremendously increased by the discovery that the lizard could be "frozen" in position by presenting it with a "snakelike" object. A straight, smooth, tapered stick about five feet long was cautiously extended until a section of it was a few centimeters in front of the anole, then it was drawn slowly back and forth in a horizontal plane. Ordinarily this caused the anole to shift his attention from the person to the stick, and to respond with a characteristic crouching reaction, Then, continuing to move the stick, the operator could maneuver into position for the catch without causing the lizard to move. The ruse was most effective when two workers collaborated.

Another method that was highly effective for terrestrial species (*Cnemidophorus deppii, Sceloporus variabilis, S. squamosus, Ctenosaura similis* juveniles) in open, level terrain such as a sandy beach, involved coordinated teamwork of two to five collaborators using strips of sheet aluminum 0.4 m wide and 1.5 m long. When a lizard was discovered, the workers would surround it, attempting to head it off from dense cover where it might escape, and to maneuver it into an open place. Then they slowly converged, with metal strips bowed and held on edge near ground level. At a signal all simultaneously lowered and advanced their strips, so that the ends overlapped and the strips formed a continuous barrier corralling the quarry. Sometimes the capture was made only after a long and strenuous chase, but under favorable circumstances as many as ten captures with two or three species were scored simultaneously as the lizards were driven along a hedge or other natural travelway into the open corral and the entrance closed at the right moment.

Lizards climbing on tree trunks and fence posts often were caught by hand. The stalker approached unseen from the side away from the lizard, after noting its position. Effectiveness of capture was increased if a second person in the vicinity kept the lizard under observation, diverted its attention, and directed movements of the stalker, especially the final grab.

Noosing was the best method of capturing some kinds of shy, fast-moving lizards. Copper wire nooses on the ends of tapered sticks or poles about 2 m long were used. Skinks (*Scincella* and *Mabuya*) and geckos (*Gonatodes*) were caught by hand.

Relatively small numbers of lizards were collected and preserved to serve as voucher specimens, and for internal examination, mainly investigation of the gonads. Testes were measured in males. Most of the specimens collected were females, and they were examined for presence of yolked follicles and uterine eggs or embryos, which were measured, and for

corpora lutea. The University of Kansas Museum of Natural History contains much Costa Rican and nearby material, some of which is of the same species that I studied, and even from the same or nearby localities. These specimens supplemented my own collections.

Study areas were sampled in a sequence which varied from time to time, and an average interval of approximately six weeks elapsed between successive samples. Because of the large number of areas involved, and the amount of time spent travelling, an average of only a little more than two days was available for each sampling.

I visited many of the study areas for the first time and made preliminary observations and collections in February and March 1965. The field studies were carried out 13 Oct. 1967 to 17 July 1968, 8 Aug. to 8 Sept. 1968, 18 Jan. to 13 March 1969, 8 Aug. to 8 Sept. 1969, and 29 Jan. to 14 March 1970.

CLIMATIC FACTORS

The broad spectrum of climates within the radius of 154 km encompassed by the study areas obviously controlled distribution, abundance and behavior of the species studied. The proximity of two oceans, and lofty mountain ranges differing in their directional trends, often produce striking climatic change within a relatively short distance. All localities were latitudinally well within the Tropical Zone, from Quepos 9° 26′ N on the south to Playas del Coco 10° 34′ on the north, and from Playas del Coco 85° 44′ on the west to Limón 83° 03′ on the east.

The Cordillera de Guanacaste, C. de Tilarán, C. Central and C. de Talamanca form a nearly continuous chain through Costa Rica from northwest to southeast, separating the hot and humid lowlands to the north and east on the Caribbean Coast from the sometimes dry lowlands of the Pacific slope. Scott (1966) emphasized the important effect of dependable northeasterly trade winds on the Caribbean versant, and the influence of seasonal winds on the Pacific versant. In this classification the study areas fall into five climatic zones, as follows:

Wet Atlantic Lowland (Portéte, Limón, Beverly; less typically, San Miguel de Sarapiquí, Turrialba and Cartago) is characterized by high rainfall relatively evenly distributed throughout the year. According to Scott, rain is almost equally probable at any time of the day or night. The cloud cover is persistent, effectively and significantly cutting down insolation, evaporation and temperatures. Average relative humidity is high, and evaporation rarely exceeds precipitation over any lengthy period. Temperatures are moderate, with relatively large daily fluctuation but little seasonal change. Scott (1966) stated ". . . Insect populations maintain themselves at a fairly constant level throughout the year." Figures 2, 3A and 4 summarize weather records for this zone.

Wet Pacific Lowland (Quepos) is characterized by high rainfall, but a marked dry season, with relatively little rain from December through April. Rain falls chiefly in the afternoon and evening. Temperature tends to be high and relatively uniform. Figures 3B and 5 summarize weather records for the Quepos area.

Dry Pacific Lowland (Playas del Coco, Sardinal, Finca Taboga, La Irma, Boca de Barranca) is characterized by high average temperature and low rainfall (especially during the dry season, December through most of April). Even during the rainy season, mornings are often cloudless, permitting a high evaporation rate, and almost all rain falls during the afternoon and night. Evaporation rate is high throughout the year, and exceeds precipitation for about eight months. There are strong north winds early in the dry season,

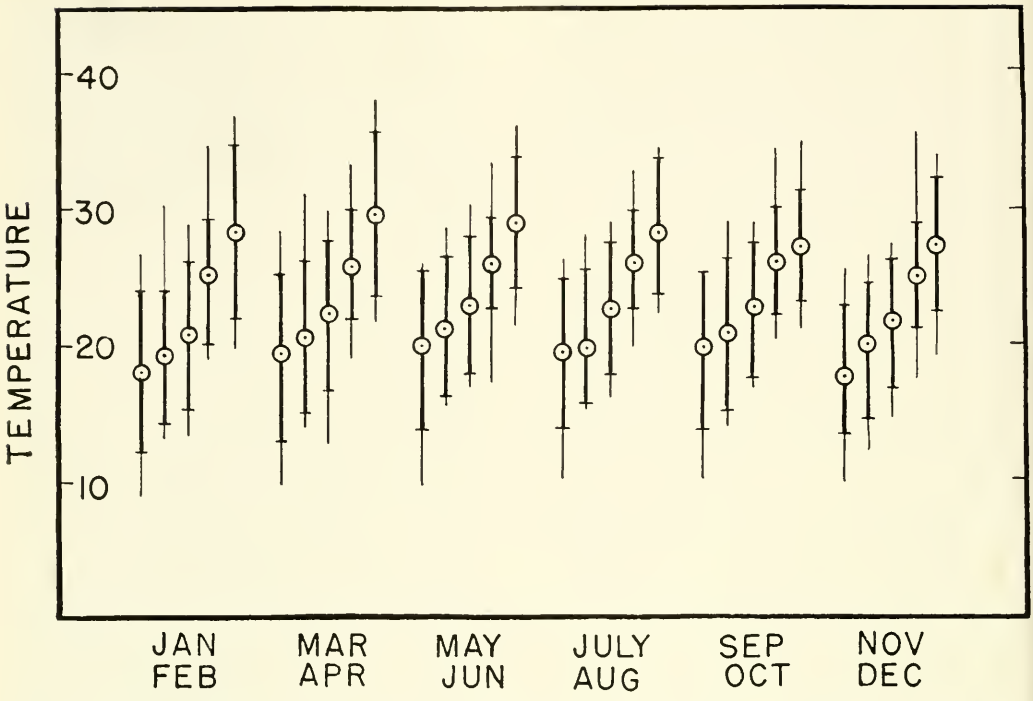

FIG. 2. Annual temperature range shown in bimonthly intervals for five sites representing six localities. From left to right in each group, vertical bars represent Cartago, San José, Turrialba, Limón, and Filadelfia (near Playas del Coco and Sardinal). For each site and bimonthly period, mean, mean minimum, mean maximum and extremes are shown (from Anuario Meteorológico, 1966, 1967, 1968, Servicio Meteorológico Nacional, Costa Rica).

December through February. For the remainder of the year winds are relatively mild and often are westerlies. (See Figs. 2, 3B and 5.)

Dry Pacific Intermediate (San José, Las Pavas) is characterized by a rainfall pattern similar to that of the Dry Pacific Lowlands but lower temperatures. The lower temperatures retard evaporation, and relative humidity remains fairly high, hence the dry season is less severe than in the lowlands. (See Figs. 2, 3B and 6.)

Wet Atlantic Intermediate (Hacienda El Prado) is characterized by high rainfall and cool temperatures the year around. Evaporation is generally low, but exceeds precipitation in February and March. High winds are frequent. (See Figs. 3B and 6.)

Statements in the foregoing paragraphs are generalizations which apply more or less to the specific study areas, but each area has its own climatic pecularities and some deviate markedly in unexpected ways from the mode of the broad zones in which they have been included. No field records of weather were kept in the course of my study, but instead records of the Servicio Meteorológico Nacional of Costa Rica were utilized. In the published annual reports of this agency data from many field stations are included, but the field stations contributing and the kinds of information provided by them differ from year to year. Also, in most instances the field stations are somewhat removed from the actual study areas and hence provide only approximations of their climatic traits.

Figures 2 to 6, based on records of the Servicio Meteorológico Nacional (1966, 1967, 1968), show climatic characteristics

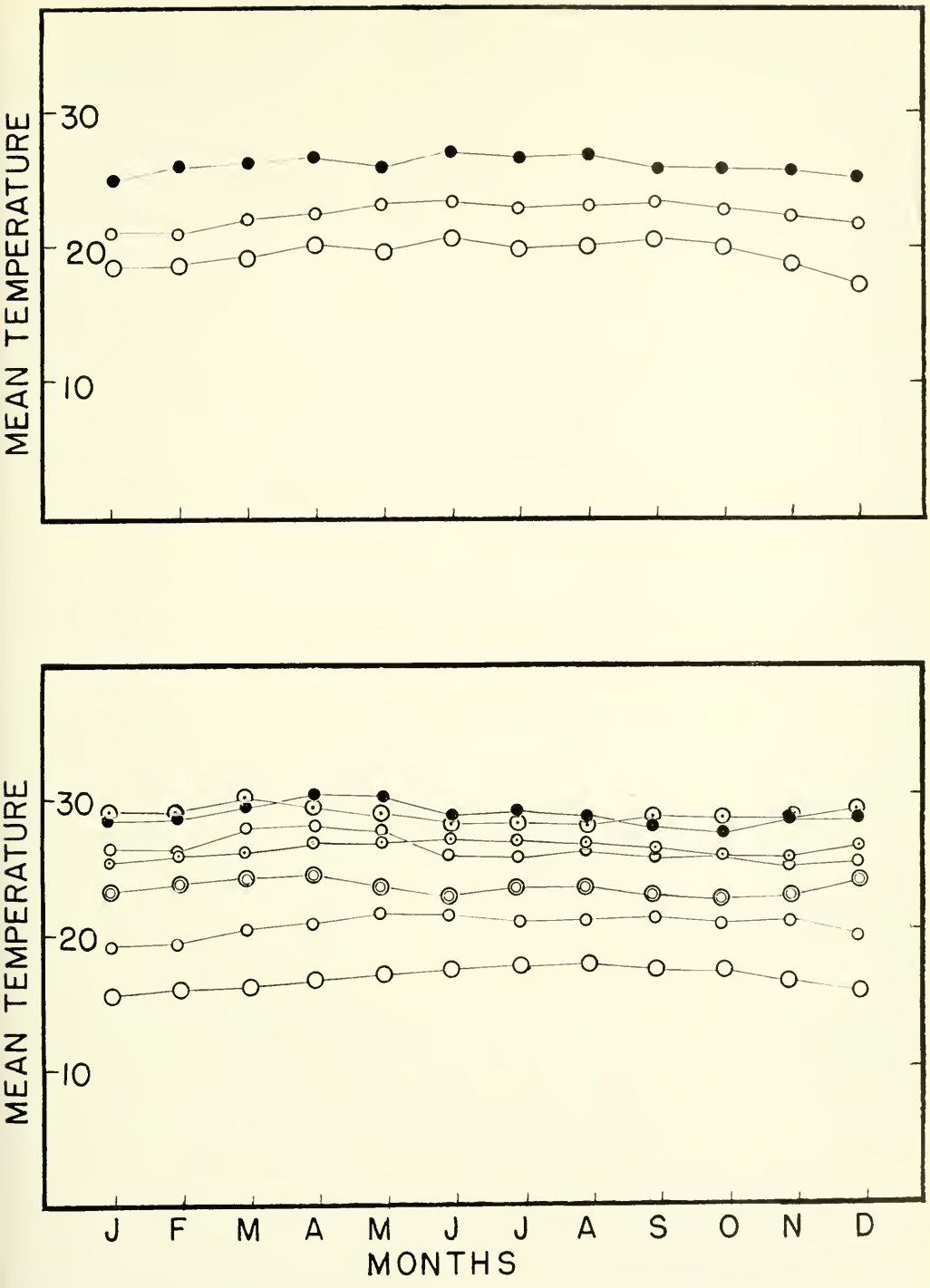

Fig. 3. A (above). Mean monthly temperatures at three localities of the Caribbean versant: solid circles, Limón; small open circles, Turrialba; large open circles, Cartago. B (below). Mean monthly temperatures at seven sites representing eight localities of the Pacific versant: small solid circles, Filadelfia (near Playas del Coco and Sardinal); large circles with dots, Puntarenas (near Boca de Barranca); small open circles (of upper series), Las Juntas (near La Irma); small circle with dot, Parrita (near Quepos); double circles, Santa Ana (near Las Pavas); small open circles (of lower series), San José; large open circles, Vara Blanca (near Hacienda El Prado). (Same source as Fig. 2.)

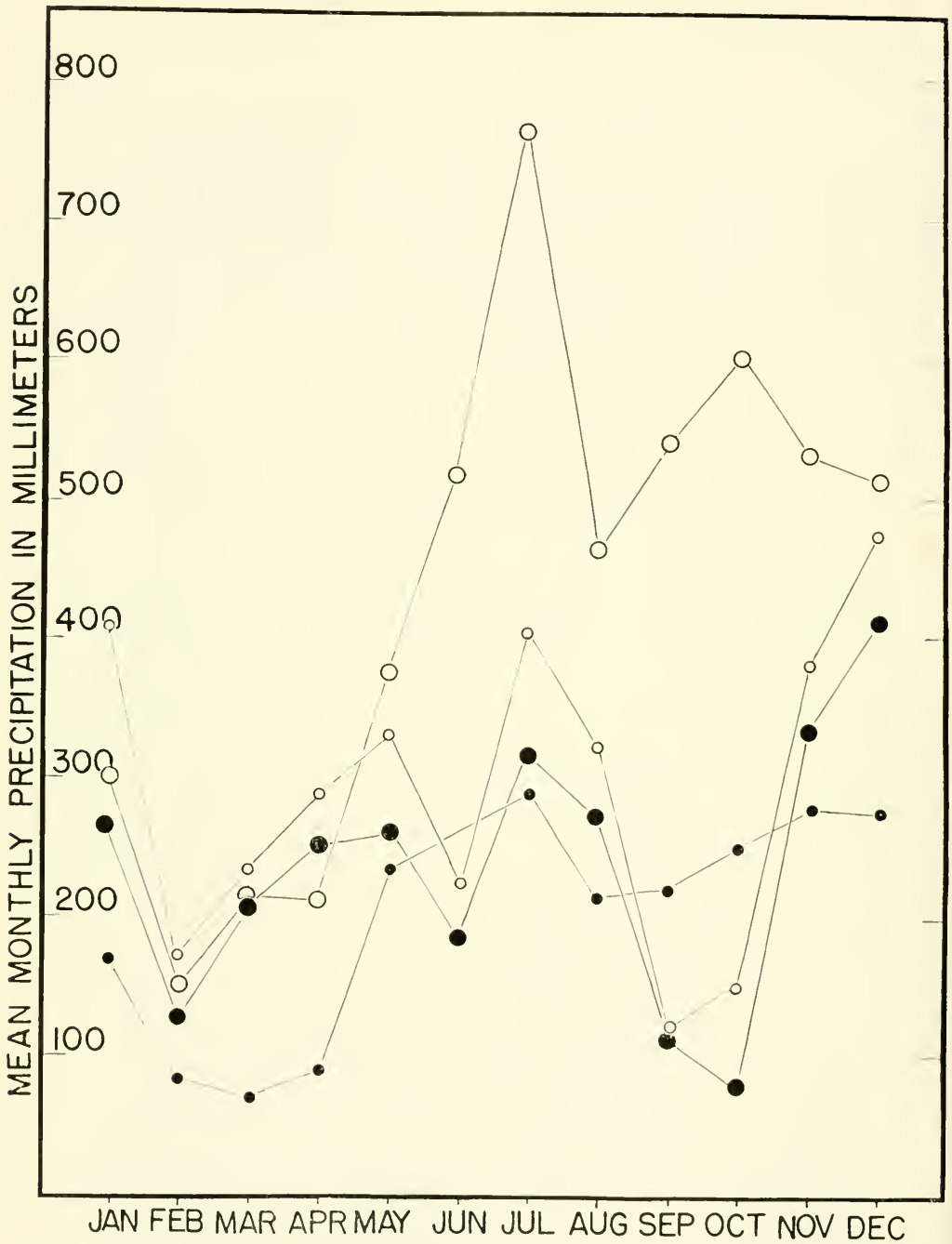

FIG. 4. Mean monthly precipitation at four localities of the Caribbean versant: large open circles, San Miguel de Sarapiquí; small open circles, Limón; large solid circles, Beverly; small solid circles, Turrialba. Records for San Miguel are five-year averages (1961-1965); others are ten-year averages (1956-1965). (Same source as Fig. 2.)

of weather stations near the study areas. The study area at Hacienda El Prado near Vara Blanca was at the Continental Divide, but was actually in the Pacific drainage. However, Vara Blanca has a climate more characteristic of the Atlantic versant

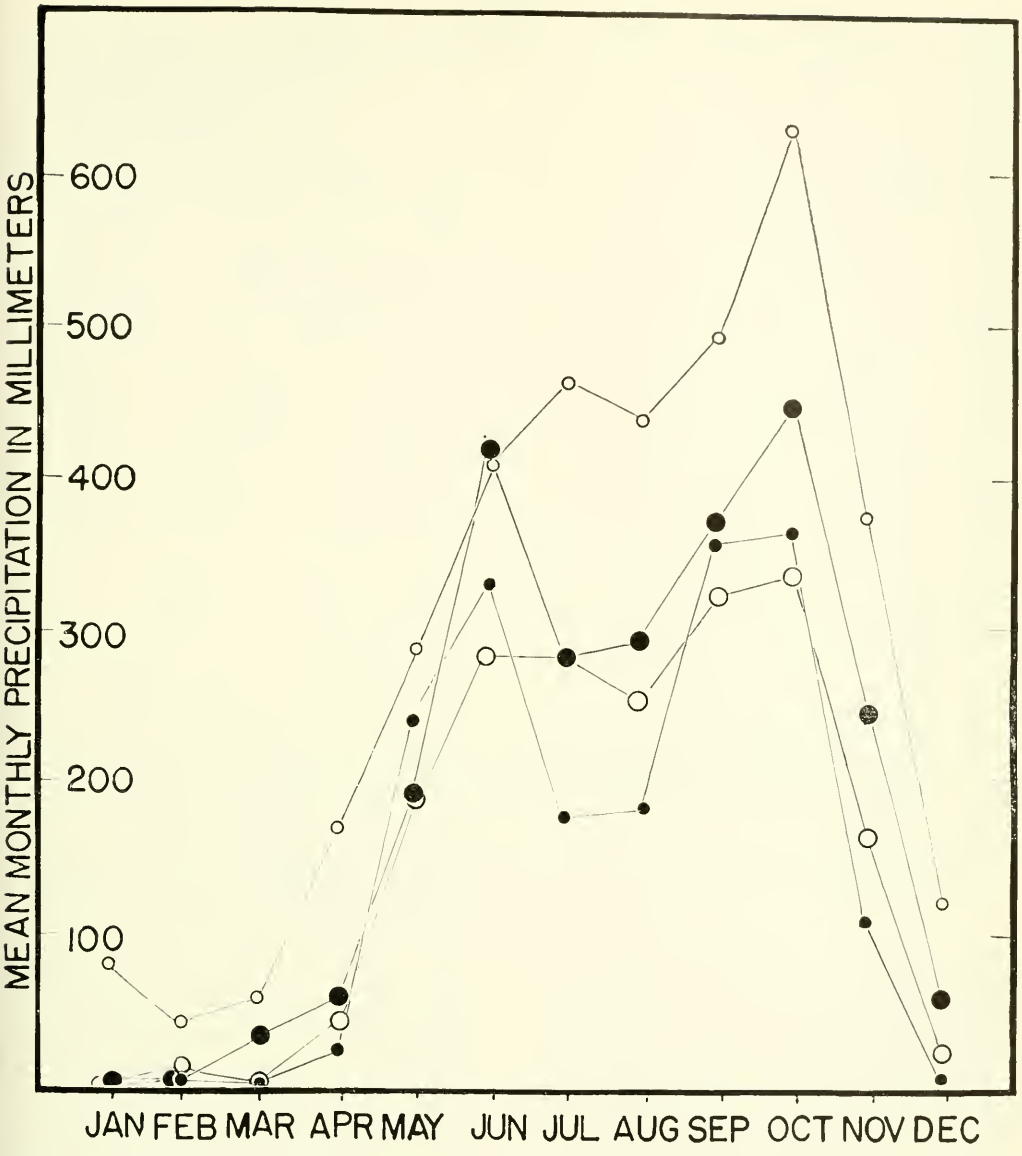

Fig. 5. Mean monthly precipitation at four sites representing five localities of the Pacific versant: small open circles, Quepos; large solid circles, Las Juntas (near La Irma); large open circles, Boca de Barranca; small solid circles, Filadelfia (near Playas del Coco and Sardinal). Records for Las Juntas are averages for years 1961 to 1965; others are averages for years 1956 to 1965. (Same source as Fig. 2.)

—high precipitation for the most of the year, including December and January. The study area represented by San Miguel de Sarapiquí is about 4 km south of the town and farther in the mountains, where climate is somewhat cooler and wetter. Cartago, situated on the Caribbean versant at medium-high altitude, could be expected to have a cool and moist climate, but the records indicate that it is remarkably dry. Annual precipitation (1961-1965) averaged only 1107.3 mm, much less than at any other station in Costa Rica. Presumably low precipitation is correlated with the presence of Volcán Irazú (3432 m) 16 km north-northeast intercepting

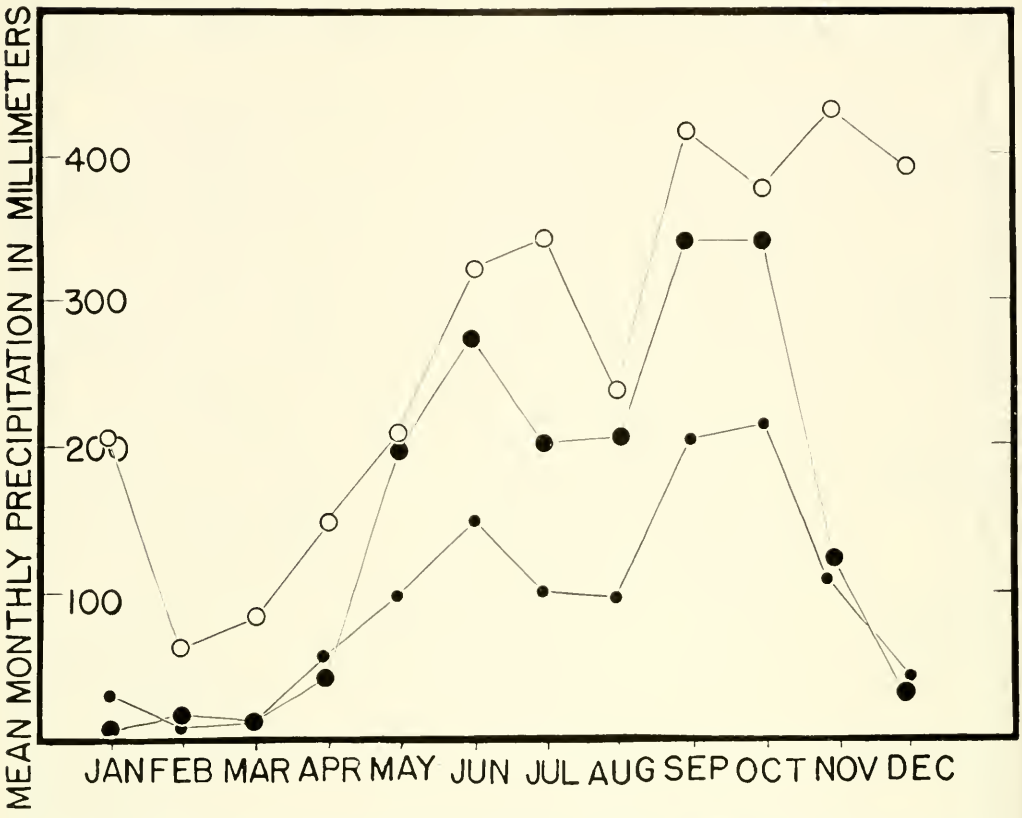

FIG. 6. Mean monthly precipitation at three sites representing localities of the Meseta Central; large open circles, Vara Blanca (near Hacienda El Prado); large solid circles, San José; small solid circles, Cartago. Records for San José are averages for years 1956 to 1965; those for Cartago and Vara Blanca are averages for 1961 to 1965. (Same source as Fig. 2.)

moisture-laden air from the Caribbean and casting a rain shadow. Turrialba, situated nearer the Caribbean Coast and at lower altitude than Cartago, has a much wetter climate, but here too the weather records show less precipitation than might be expected, and the mountain mass of Volcán Turrialba (3328 m) 16 km approximately northwest probably affects local rainfall to some extent. Portéte on the Caribbean Coast just west of Limón, and Beverly 12 km south on the coastal plain show almost identical trends in annual precipitation, but with consistently greater amounts each month at Portéte. There are definite peaks in May, July and December, with relatively meager precipitation in February, June and September-October. San Miguel de Sarapiquí, situated on the lower slopes of Volcán Poas on its Caribbean side, has one of the wettest climates in the country, but rainfall is subject to marked seasonal change, with a peak in July and relatively meager precipitation in February, March and April. Playas del Coco and Sardinal are believed to be adequately represented by the records kept at Filadelfia 20 km and 14 km SE, respectively, but Filadelfia is somewhat more removed from the moderating influence of the ocean. The study area at La Irma, Río Congo, is represented by the station at Las Juntas approximately 4 km distant, but Las Juntas is 100 m higher and probably has a somewhat cooler and wetter climate. In the Pacific lowlands (Filadelfia, Las Juntas, Boca de

Barranca) the peak of the rainy season is in October and dry season extends from December through April. A characteristic feature is the *veranillo,* a minor dry season in July and August which separates the peak precipitation of October from a lesser peak in June. The *veranillo* is scarcely noticeable in the records from Quepos, which has a much wetter climate than the other localities of the Pacific lowlands. Quepos is allocated in the Pacific Wet Lowlands, but has much less precipitation than lowlands of extreme southeastern Costa Rica; actually it is in a zone that is transitional between this area and the Pacific Dry Lowlands of northwestern Costa Rica.

STUDY AREAS

Field work was conducted on 23 separate study areas (not all used concurrently) at the 15 localities shown in Figure 1. Kinds of lizards present and the numbers of them recorded at each locality are shown in Table 1. Areas differed greatly in size and shape, and in stability of their lizard populations. The areas were originally chosen on the basis of having high populations of lizards, of being relatively accessible, and of representing distinct types of habitat and climate. During my field work most of the original study areas were grossly disturbed—by flood and high tide in some instances, but usually by human activities such as tree-cutting and bulldozing, resulting from rapidly expanding population and industry. Such occurrences seriously hindered my studies and necessitated change in the routine of sampling and, sometimes, transfer of operations to other areas. Areas utilized were the following:

Playas del Coco, Guanacaste Province, 1-3 m. Two study areas selected were similar fenced seaside lots (without buildings) in a resort subdivision. Area no. 1 was 107 m x 32 m but its southeastern part, 55 m x 10 m, was a dense thorny thicket, which was excluded. A lane 8 m wide on the south edge of the original study area, and the fence bounding an adjacent lot, were incorporated after the first sampling. The area extended inland from the crest of the beach dune. Near the crest were low patches of sea grape *(Coccoloba uvifera).* A hedge of cactus-like euphorbiaceous plants 2 to 3 m high bounded the lot on its ocean front to the west and on the south side and part of the north side. The part nearest the ocean was a sand field with three large tamarinds *(Tamarindus indica)* and with open areas of low weeds, and bare ground riddled with the burrows of land crabs. The field sloped to a bare swale which sometimes held water in the rainy season. Beyond the swale the lot was wooded. There were six coconut palms *(Cocos nucifera)*; a tree of *Cassia grandis* nearly 1 m in trunk diameter dominated the eastern part, and there were smaller trees of *Delonix regia, Terminalia catappa* and *Spondias* sp. Early seral herbs, and shrubs such as ant plants *(Acacia cornigera)* were abundant.

Cnemidophorus deppii was abundant, especially on the more open and sandy part, and at the front hedge. *Sceloporus variabilis* was common on and near the larger trees and some lived in the hedge or on fence posts. *Ctenosaura similis* tended to keep near the larger trees or the denser parts of the hedge. *Ameiva undulata* stayed in or near the thicket in the northeast part of the lot. *Anolis cupreus* was occasionally found on stems of shrubs or low on the trunks of the smaller trees. Several *Sceloporus squamosus* were found in the lane bordering the lot and in adjacent barren fields. *Anolis sericeus* was rare; the few individuals found were on fence posts in more open situations than those frequented by *A. cupreus.*

Ctenosaurs were occasionally hunted

on the area by persons armed with small bore rifles or by children with dogs. Otherwise there was little direct effect on the lizard populations by humans. Many vehicles and pedestrians moving up and down the beach passed along the front hedge. At intervals of several weeks, crews of *macheteros* cleared brushy and thorny low vegetation, which was stacked and burned, probably eliminating some lizards that had resorted to the piles for shelter. Horses, hogs, dogs, and chickens ranged over the area. Wildlife was not abundant; potential predators on lizards that were noted were the armadillo *(Dasypus novemcinctus),* the Magpie Jay *(Calocitta formosa)* and a snake *(Conophis lineatus).*

Area no. 2 was 35 m x 31 m and was chosen for study of *Sceloporus variabilis,* but most species noted on no. 1 were present here also. This lot was 1 km farther north than no. 1, near the end of the beach, and there was little human activity. The study area was the front (west) half of a lot dominated by two *Bombacopsis quinata* trees 2 m and 1.3 m in trunk diameters (Plate 1, lower). Seven trees of *Delonix regia* averaging 0.2 m in trunk diameters were distributed over the area. Other small trees or shrubs included *Coccoloba* sp. and *Terminalia catappa.* Weedy shrubs, especially ant plants, were abundant. Clumps of low vegetation provided effective refuge for the lizards.

Gonatodes albogularis was not seen on either study area, but was abundant on several large strangler fig trees (*Ficus* sp.) and occasionally on smaller trees, fence posts, walls and rocks along the southern part of the beach where human activities were most concentrated.

Sardinal, Guanacaste Province, 90 m. The study area was approximately 0.5 km northwest of the village, and extended 100 m up a ravine from its outlet into the Río Sardinal. The ravine ran parallel to a road on its south side. Cultivated fields were on both sides, and nearby slopes were heavily grazed, with vegetation of xeric aspect, but the ravine and its vicinity were more mesic, with a remnant forest including giant trees of *Terminalia* and other kinds forming a band about 50 m wide. The ravine had steep banks, usually 3 m or more high. In the dry season there was little more than a seepage in the ravine bottom, and even in the rainy season there was usually only a small volume of water flowing. Leaf litter carpeted the ground and accumulated in thick masses along the ravine bottom, but bare soil was exposed along the steep banks. Dense brush and luxuriant herbaceous vegetation grew in some places, but was periodically trimmed at the edges of the fields by *macheteros.* Barbwire fence separated the grove from adjacent fields. Humans were rarely seen on the study area, but many passed on the road either on foot or on horseback. Hogs and occasional horses and cows were on the study area. The Roadside Hawk *(Buteo magnirostris)* was occasionally seen and frequently heard in the grove. *Anolis cupreus* was extremely abundant in and along the ravine and was the main species studied. *Ameiva undulata* was common in the grove and along the edges. *Ctenosaura similis* was moderately common. *Gonatodes albogularis* was often seen on bases of the large trees and on fence posts. *Basiliscus basiliscus* was occasionally seen in the ravine and was abundant along the river nearby. *Iguana iguana, Sceloporus variabilis, Sceloporus squamosus, Anolis sericeus,* and *Cnemidophorus deppii* were seen from time to time.

Finca Taboga, Río Higuerón, Guanacaste Province. The area was on the coastal plain near sea level. From a bridge across the river the study area extended in one direction approximately 1 km upstream where the diked and channelized stream flowed through cleared pastureland with tall rank grass. A second segment

extended through swampland forest from approximately 2 km to 4 km below the bridge. This lower reach of the river was much less altered and the channel followed a meandering course. Giant trees, guanacastes *(Enterolobium cyclocarpum)* and others, were numerous, but much of the vegetation was scrubby and thorny. Oxbows, marshes and ponds alternated with higher ground. Flooding was extensive in the rainy season. The river's course was frequently obstructed by log jams and large fallen trees. Banks were frequently undercut, with exposed tree roots or vine tangles. The river was often 5 to 10 m across and 0.5 to 2 m deep.

Basilisks were abundant along both stretches of the river, and were concentrated where shelter was most plentiful. Iguanas were numerous, especially in the swamp forest. Ctenosaurs were seen mostly in dry pasture land. Under favorable conditions many were seen from the road.

The Finca Taboga area was less densely populated by humans and was less subject to gross disturbance than most of the other areas studied. However, crews of laborers were regularly trucked to the area for work in cultivated fields, for machete clearing of pasture land or less frequently for fence building or road construction in the swamp. Here as elsewhere, ctenosaurs and iguanas were subject to some persecution, but their numbers were seemingly not much affected. Wildlife abounded in the area. Doubtless many kinds of mammalian predators were present, but predatory birds were much more in evidence. These included the Crested Caracara *(Polyborus cheriway)*, Laughing Falcon *(Herpetotheres cachinnans)*, Common Black Hawk *(Buteogallus anthracinus)*, Gray Hawk *(Buteo nitidus)*, Roadside Hawk, Broad-winged Hawk *(B. platypterus)*, Wood Stork *(Mycteria americanus)*, Common Egret *(Casmerodius albus)*, Great Blue Heron *(Ardea herodias)* and many others. Snakes observed included *Boa constrictor*, *Conophis lineatus* and *Crotalus durissus*.

La Irma, Río Congo, Guanacaste Province, 100 m. The study area was along the river approximately 1.5 km NNE of La Irma. Land was cattle range of rolling hills, with occasional large trees or patches of scrubby forest. A mesic gallery forest followed the stream intermittently with trees of *Terminalia* and others, some of giant size. Between gentle slopes the stream followed a meandering course in a narrow bottom with a gravel bed and occasional sand deposits. There were cutbanks, sometimes as much as 3 m high, bare or with exposed tree roots or sometimes mantled with vines and other luxuriant vegetation. In other places the terrain sloped gradually to the edge of the water. Series of shallow riffles alternated with deep pools. Many of the trees grew at the edge of the bank, with roots on one side exposed or undermined. Flow was highly variable. In the rainy season the river often overflowed its banks and cut new channels, whereas in the dry season the flow between pools was reduced to a trickle. In times of flood massive deposits of drift accumulated in log jams (Plate II, lower) and on the banks. On most of my visits the flow between pools was 0.1-2 m deep and 1-5 m wide.

At this locality, greatest effort was devoted to a study of *Basiliscus basiliscus;* it was hunted along the stream for a linear distance of approximately 0.5 km, but because of the winding course of the stream, the opposite ends of the study area were only about 150 m apart. *Anolis cupreus* was found in phenomenal abundance in a strip within a loop of the creek on its left bank, an area approximately 50 m long and 15 m wide. In June 1968, after heavy flooding, however, lizard populations were much reduced.

The entire area was heavily grazed and trampled by cattle, but there was little human activity. Horsemen occasionally rode across it and on several occasions hunters with firearms were seen stalking iguanas. Wildlife was abundant. Howler monkeys *(Alouatta palliata)* were seen or heard many times daily. Predators that might have affected lizard populations were numerous and included hawks *(Buteo magnirostris),* and herons *(Ardea herodias, Casmerodius albus).*

Boca de Barranca, Puntarenas Province, 1-3 m. Two separate study areas, each with several parts, were used. The first area centered on the grounds of the Marbella Hotel, a beach resort on the north side of the Río Barranca at its mouth. The hotel buildings were situated on the front dune only a little above high tide mark. They included a large pavilion, dormitories, and various accessory small buildings. The hotel grounds extended 220 m along the beach and 140 m back from the crest of the dune. Numerous coconut palms and other trees both native and exotic were scattered over the grounds (Plate II, middle). There were two giant tamarind trees, flower beds, weedy and grassy areas, lines of boulders along the entrance driveway for 150 m, piles of trash mainly of coconut fronds that were periodically burned, and other more permanent trash heaps of scrap metal, broken glass and a variety of wooden and plastic articles. The sand beach on the ocean side of the hotel grounds varied in extent and conformation, being frequently altered by high tides and storm. Sea grapes and tall coarse grass stabilized parts of the dunes and provided some shelter. Beach wrack consisting of logs, boards and sticks with an intermixture of discarded articles was especially abundant near the river mouth. At high water mark, masses of wrack accumulated, interwoven and anchored by logs and palm fronds partly buried in the sand, and providing an abundance of hiding places for lizards and other small animals. North of the hotel grounds a series of private resort homes, each on a lot several acres in extent, faced onto the beach. Some of the lots were enclosed by fences. Some had groves of ornamental or fruit trees. *Sceloporus variabilis* was studied not only on the hotel grounds but along the line of beach wrack (Plate II, upper) for nearly 1 km to the north. *Ctenosaura similis, Cnemidophorus deppii,* and *Gonatodes albogularis* were studied mainly on the hotel grounds, where all of them were abundant.

On weekends and especially during the holiday season of February and March, vacationers, greatly outnumbering the resident population, visited this resort. Occasionally boys with slingshots, air rifles or firearms killed lizards. Ctenosaurs especially were subjected to constant persecution, being considered pests because of their digging activities, and were also hunted for sport and for their edible flesh and unlaid eggs. Dogs, cats, hogs, chickens and turkeys ranged freely over the hotel grounds and all of them preyed upon lizards. Chickens and cats especially were believed to have reduced the numbers of some kinds of lizards and perhaps had eliminated *Anolis cupreus* which was not found on the hotel grounds.

The second area, on the south side of the river's mouth, was allotted relatively little time and *A. cupreus* was the only species studied there. A steep hill overlooked the river and there was a series of small inlets with narrow sandy or rocky beaches and steep banks or cliffs rising precipitously from the shoreline. A scrubby xeric forest with many kinds of native trees, shrubs and vines extended down to the ocean edge at the base of the bluff. The area was little altered by human activity. A few isolated shacks of fishermen and other residents were scattered along

the lower end of the river, and on holidays and weekends picnickers and hikers crossed the river in rented rowboats.

Quepos, Puntarenas Province, 0-70 m. Field work was concentrated in a beach area 3-4 km northwest of the town and just south of the mouth of the Río Cañas. Here there were extensive stretches of open sand, and quantities of wrack carried down by the river had accumulated at high tide level. Cordgrass formed a mat over the dunes in places. Groves of coconut palms grew on the crest of the dune and its lee side down to the edge of a mangrove swamp. Banana plantations occupied part of the dune. At the north end of the dune beyond the plantations an area of natural vegetation estimated as 2 hectares bordering the swamp had a dense thicket of cane and spiny palm. There was little human activity on the area but occasionally fishermen, bathers, and hikers crossed it, and charcoal burners sometimes worked there. Individuals or small groups occasionally came to hunt iguanas with guns and dogs. *Ameiva quadrilineata* was the main study species. These lizards were difficult to catch but easy to observe. During late spring and summer young ctenosaurs were abundant.

Hacienda El Prado, Alajuela Province, 1910 m. The study area of 2 hectares was approximately 5 km west of Vara Blanca and was bounded on the north by Costa Rica Highway 120, here following the Continental Divide in montane cloud forest on the southeast slope of Volcán Poas. The area was used as pasture and the original forest of *Oreopanax jalapensis, Drimys, Quercus, Trema, Turpinia, Eugenia, Sloanea, Bocconia, Spondias* and other trees had been largely destroyed, but there were scattered living trees, some of giant size. A spongy mat of dense grass, often 0.1 m thick, covered the ground, and logs, stumps and tree trunks similarly supported a luxuriant, spongy growth of epiphytes of many kinds.

Fenced pastures within the study area were alternately subjected to heavy grazing and then retired from use for periods of weeks. Workers periodically trimmed back sprouts and epiphytes, checking the spread of woody vegetation. On 21 Jan. 1969 clearing operations were in progress and most of the remaining large trees on the area were cut and burned, drastically reducing the numbers of lizards. The only potential predator noted on the area frequently was the Brown Jay *(Psilorhinus morio). Anolis tropidolepis* was the main species studied; *A. intermedius, Sceloporus malachiticus,* and *Gerrhonotus monticola* were found infrequently. Some of the records for all four species were obtained on a nearby area of similar habitat 1 km south of Vara Blanca (Heredia Province) in October and November 1967 and January 1968.

San Miguel de Sarapiquí, Alajuela Province, 500 m. This study area was on the northeast slope of Volcán Poas, beside Highway 9, between San Miguel and Cariblanco, and on a west branch of the Río Sarapiquí 100 m upstream from where the highway crosses the river. The lower half of the study area was essentially an island in this stream, but on the right side of the main channel. The upper part of the area was along the streambank. The stream was swift and clear in a rocky bed, with gravel and cobble along its edges and with many protruding boulders. The stream was usually 0.5 to 2 m deep, with steep banks, and a fairly stable flow of water. Rain forest vegetation covered the study area. There were large trees of many species, with buttressed roots; tree trunks and limbs were heavily laden with epiphytes, especially bromeliads. Moss and lichens grew in a thick carpet on tree trunks and rocks. Lianas were abundant. Ground was covered with a carpet of dead leaves and also supported a luxuriant growth of low herbaceous broad-leafed

vegetation except where high water had swept away vegetation and debris. Masses of drift and debris accumulated over obstructions. The study area was 150 m long and 10 to 50 m wide, bordered for part of its length by a long, narrow strip of bottomland pasture and for the remainder by precipitous slopes.

No humans were ever seen on the study area, and presumably it was so rarely visited that persons had little direct effect on its lizard populations. Access from the road was hindered by steep slopes with cliffs or by the swift and deep current of the stream. Horses and cattle occasionally ranged over the study area. No other domestic animals were known to visit it. Wildlife including predators was probably common, but animals were not readily seen or heard because of the dense cover and the roaring of the swift water.

San José, San José Province, 1197 m. Several study areas were used in the eastern part of the city, but they changed throughout the course of field work. Although lizards were abundant at certain times and places, the expanding human population and booming economy frequently caused their disturbance or destruction in the places chosen. One area extended along the right-of-way of the Northern Railway west southwest from Highway no. 202 (near the University of Costa Rica campus) about 1 km, to Calle 39. For most of this distance the railway was bordered by groves of coffee trees. Barbwire fences utilizing living trees (usually *Gliricidium*) as posts (Plate 1, upper) separated the railroad strip from private property adjoining. Tall grass grew in the ditches along the railroad bed and the fences. Occasionally machete crews cut the grass and trimmed the sprouts on the *Gliricidium* tree fence posts. Lizards were found chiefly on the fence posts, sometimes on trees, including the coffee trees and larger shade trees in the cafetals. *Anolis cupreus* was nearly always the most abundant, and was the main object of study. *A. intermedius* was usually less numerous, but it outnumbered *A. cupreus* along a line of yuccas fronting a coffee factory for 100 m. *Sceloporus malachiticus* was present in relatively small numbers.

A second major study area was 200 m south of the east end of the first in the large lot of the Eldorado Apartments. Many trees grew in the lot, which was bounded on the north by a fence and cafetal, and on the west by a concrete wall. In the northeast corner was an extensive pile of tree cuttings and trash. From time to time crews of workers cut the grass and trimmed the sprouts on the trees. By June 1968 lizards had become relatively scarce, both along the railroad and at the lot.

Population samples were subsequently obtained from several other areas as follows: 1) a lot at the corner of Avenida Central and Calle 29, about 50 x 50 m. *Anolis cupreus* was found on fence posts and walls around the edge. 2) A large vacant lot south across Avenida Central from the Eldorado Apartments. This lot had many large trees and had a remnant of a coffee grove along its east edge. It was especially productive of *A. intermedius* when first sampled in August 1968, but in March 1969 trees were cut and the lot was bulldozed, resulting in the virtual extermination of the lizards. 3) A small lot 200 m south of no. 2, in the Montes de Oca district. This lot was traversed by a ravine with a small stream, and high weeds and grass grew on it. Alice Fitch Echelle marked many *A. intermedius* and *A. cupreus* and made observations on their behavior from March through June 1968. 4) A lot at Avenida 12 and Calle 25 where population samples of *A. cupreus* were collected from time to time in 1968, 1969 and 1970. 5) A large lot on the north side of Avenida 10 and west side of Calle 27

first sampled in June 1968 and subsequently made the basis for marking operations in 1969 and 1970. Eventually it yielded more records than all the other areas combined. For much of its perimeter this lot was enclosed by cement walls, and tall coarse grass grew over most of it. *A. cupreus* and a few *S. malachiticus* were found chiefly on the lower parts of the walls and at their bases, and were found in trees, shrubs and grass tussocks, but relatively few were found in open areas.

All the study areas were surrounded by human dwellings and use of the areas by humans was heavy. Trampling and littering with discarded objects of many sorts affected the habitats. Also at times persons made active search for lizards to destroy them. Our own activities tended to draw attention to the lizards, and probably increased this sort of mortality. Cats, dogs and rats *(Rattus rattus)* were often seen on the study areas and may have preyed on the lizards occasionally. Of native animals that were potential predators, the Brown Jay was the only kind noted frequently. Insecticides, including chlorinated hydrocarbons, were being heavily used in San José at the time field work was in progress. Especially in the cafetals, heavy spraying may have caused direct poisoning of the lizards or may have affected them by ingestion of poisoned insects. Although success in hunting the lizards was much affected by the weather and recent cutting of thick vegetation, it is certain that the population on each area underwent drastic reduction at one time or another in the course of my work, and poisoning by insecticide seemed the most plausible explanation except in cases where the habitat was destroyed or grossly altered.

Las Pavas, San José Province, 1100 m. The study area was 2 km northeast of the village which is a suburb on the west side of San José. In an urbanization program an area of several hectares had been subdivided into city blocks, with paved streets, poles for street lights, and sewers, but with only a few occupied houses, and with grass and weeds over the lots. A cafetal extended along the north side of the subdivision. Where a road entered the cafetal, a colony of *Ameiva undulata* was found and many were caught and marked within a radius of 30 m in April 1968. On later visits the small colony on which efforts had been concentrated had been largely destroyed or dispersed as a result of bulldozing. *Anolis cupreus* and *Sceloporus malachiticus* were both present at this locality, but relatively few records of them were obtained. A few horses and cattle ranged over the area. Stray dogs and cats were fairly common, and may have preyed on ameivas in some instances. Brown Jays were seen and heard frequently; otherwise native predators were scarce.

In February 1969 it was belatedly discovered that *Basiliscus basiliscus* was abundant in the gorge of the Río Aguilar immediately south of Las Pavas, and subsequently several visits were made to record population samples from sight records. Sides of the gorge were so precipitous that human activity was largely excluded, and a luxuriant, nearly impenetrable growth of native trees, shrubs, vines and herbs grew there. The bed of the river was boulder strewn, with a series of rapids. The stream was dammed opposite the town, and a cement-lined ditch diverted water from it along the north wall of the gorge. The outer bank of the ditch provided a trail along the side of the gorge, overlooking the river, but becoming progressively higher above it farther downstream. Basilisks on rocks along the river's edge for a distance of about 1 km downstream from the dam were recorded.

Cartago, Cartago Province, 1450-1750 m. This study area was chosen for an investigation of *Sceloporus malachiticus* and

no other lizards were seen on it. Because the lizard population was sparse and the lizards themselves were excessively wary and hard to capture, the study area was extensive and was never precisely defined or limited. Instead, on each visit a somewhat different area was covered—wherever a population sample could best be secured. The area was north of the town, beginning at the west end of the bridge across the gorge of the Río Reventado and extending north along the road toward Bandellira for approximately 2 km. This road paralleled the river gorge, climbing the lower south slopes of Volcán Irazú. The gravelled road meandered back and forth in a wide grassy lane and paths used by pedestrians, horseback riders or cattle paralleled the road or made short-cuts between its loops. Granitic outcrops and boulders were prominent and provided lookouts and shelters for the lizards. Heavily grazed pastures with scattered outcrops and with thickets and clumps of spiny shrub bordered the lane. The wind-swept slopes also supported small scrubby trees, some isolated and some in compact groves. Sampling extended into the adjacent pastures, especially along a pipeline where rocks were exposed. The pipeline extended west to a flat pasture area adjacent to the northwestern part of the town, which had many boulders and outcrops around its margin. This flat area provided more records than the original roadside strip in late 1968 and early 1969, but in late 1969 it was being utilized for construction of factories and the population of lizards had been eliminated. In January 1970 the original study area along the gravelled road also was found to be grossly disturbed by a road construction program.

During most of the period devoted to the study, there was little disturbance by humans. Many motor vehicles, horsemen and pedestrians passed along the road through the study area, but insofar as known they did not affect the lizard population except by momentary disturbance. Cattle, horses and dogs moved through the area frequently. Stray cats were not seen. Natural predation probably was the one most important factor in eliminating lizards from the study area. Potential predators noted include: the coyote (*Canis latrans*, here at the southern extremity of its range), long-tailed weasel (*Mustela frenata*, several seen), Brown Jay (seen and heard frequently), Broad-winged Hawk and other unidentified hawks. *Thamnophis proximus* was the only snake found on the study area that was large enough to prey on *Sceloporus*.

Turrialba, Instituto Interamericano Ciencias Agricolas (IICA), Cartago Province, 602 m. This area, on a knoll near the Institute headquarters, had trees mostly 0.1 to 1 m in trunk diameter. Low grass and herbaceous vegetation carpeted the ground and was cut periodically. There were a few rock outcrops and large boulders. *Anolis limifrons* was abundant on the tree trunks and often was found on the ground near trees. *Scincella cherriei* was fairly numerous in low vegetation. When the area was revisited on 8 June 1968 it was found to have been devastated by bulldozing and tree-cutting. Most of the trees had been removed and operations were still in progress. Lizards of both species had become scarce. Marking was discontinued and population samples were sought in a new area on the Institute grounds about 0.5 km farther north, in experimental tree plantations. *S. cherriei* was found mainly in leaf litter in a cacao grove and *A. limifrons* was found in more open plantations where there was ground cover of herbaceous vegetation. Other lizards seen in relatively small numbers included *Anolis humilis, A. biporcatus, A. carpenteri, A. lionotus, Ameiva festiva, Lepidoblepharis xanthostigma* and *Basi-*

liscus plumifrons. *Anolis biporcatus* was found in the same habitat with *A. limifrons*, but was more arboreal and much scarcer. *A. humilis* and *A. carpenteri* were found along the edge of the Río Reventazón. *Ameiva festiva* was found in small numbers in the cacao grove where ground litter was abundant.

Although the experimental plantations and diverse habitats created conditions favorable for lizards, human activity was relatively concentrated, and habitat changes were rapid. Crews of laborers were constantly in the field. Also, there was some use of insecticides on the experimental plots, and at times this may have had devastating effects on lizard populations locally. On 27 Aug. 1969 *A. limifrons* had become much scarcer than on any previous occasions in all the areas when they had been hunted previously.

Dogs were the only domestic animals seen on the study areas and they were not observed to molest the lizards. Brown Jays were often seen and heard. Snakes were probably the most important predators on the lizards, and those found included *Pliocercus annellatus, Drymobius margaretiferus* and *Leptodeira* sp.

Limón, Limón Province, 3 m. The city park was utilized as a study area for the gecko, *Gonatodes albogularis*. A population which must have totalled several hundred lived on about a dozen giant fig trees (*Ficus* sp.). A few others lived on palm trees, rocks or posts, but the fig trees with their massive trunks, buttressed roots, and innumerable holes and crevices were superior habitats. Each tree had its own colony but doubtless there was occasional wandering of individuals from tree to tree. Flower beds, ornamental shrubs and trees of many kinds were present, with wide footpaths having concrete benches along them. Many persons were usually present in the park, the number varying according to the time of day and day of the week. Native birds were fairly numerous in the park, but most of these were small kinds and natural predators were virtually absent.

Portéte, Limón Province, 1-2 m. The study area was a beach resort about 5 km west from Limón, bordering a small bay with semicircular stretch of sand and coral beach several hundred m long. A clubhouse and several cabins were on lots along the beach. A paved road to Limón was inland from the beach 40 to 150 m. The strip between the road and the ocean had groves of coconut palms. Over much of it there were jagged coral rocks, exposed or scantily clothed with vegetation, but part of the area was low and swampy with muddy deposits, hydrophytic vegetation, and often standing water. Rotting piles of old coconut husks were distributed over the area. *Basiliscus vittatus* and *Ameiva quadrilineata* were the species studied, but the latter was much less common and on some visits was not seen at all because of unfavorable weather. *A. festiva* was present where there was relatively dense ground vegetation. *Gonatodes albogularis* occurred on the bases of coconut palms. *Anolis limifrons* was present in small numbers on shrubby vegetation and tree trunks. Human activity probably had little effect on the lizards of the area, though at times there was heavy use by bathers and picnickers. Dogs and a few chickens ranged onto the area, but probably without much effect on the lizards. Snakes were probably the most important predators. Those found included *Leptophis ahaetulla, Rhadinea* sp. and *Pseustes poecilonotus*.

Beverly, Limón Province, 2-4 m. The original study area was located approximately 16 km south of Limón, on the farm of Dan Sargent. This area was essentially a strip 200 m long on both sides of a fence line that separated a marshy pasture from a cacao grove, long neglected and

overgrown with natural vegetation including trees, shrubs, lianas and broad-leafed herbs. The species studied were chiefly *Anolis limifrons* and *A. humilis*, with relatively small amounts of information obtained for *Ameiva festiva, Gonatodes albogularis*, and *Lepidoblepharis xanthostigma*. *Anolis limifrons* was abundant along the fence and at the edge of the field. *A. humilis* was not found in substantial numbers until 23 Jan. 1968; then greater effort was devoted to finding it in the cacao grove, especially around the bases of several giant native trees with buttressed roots. On 8 May 1968 much of the study area had been seriously disturbed by cutting of part of the cacao grove and the natural vegetation growing with it. In compensation the study area was then extended to include a number of large native trees along a sluggish stream adjoining the north end of the original strip. However, on 28 Feb. 1969 the study area including the newer part had been further disturbed by tree-cutting and clearing. Marking operations were then discontinued on the Sargent farm and subsequent population samples were collected about 2 km farther south, in extensive cacao groves immediately north of the railroad stop at Beverly.

ACCOUNTS OF SPECIES

Plan of Presentation

Findings are set forth under a series of species-accounts. The latter are divided by subheadings—*description, range and habitat, general habits, growth, spatial relationships, temperature relationships,* and *reproductive cycles.*

Description in each instance is a highly condensed account mentioning a few of the most outstanding characters of bodily proportions, scalation, color and pattern, and how these vary individually, or according to sex, age or season. Much more detailed descriptions of most of the species can be found in publications such as Taylor's (1956) account of the lizards of Costa Rica. The purposes of my descriptions are: 1) to impart to the uninitiated reader some idea of the sort of animal involved, 2) to indicate sexual or ontogenetic differences hitherto unrecognized or inadequately described, and 3) to enable identification of animals. In view of the possibility of unforeseen taxonomic problems, the descriptions are intended to leave no doubt as to which species were involved in the field work. For most kinds, sizable series of voucher specimens have been deposited in the University of Kansas Museum of Natural History collection. An essential part of the description for each species consists of length measurements (and weights in some instances) listed in Table 2.

Range and habitat. A general statement of geographic range is made on the basis of records in the literature and my own field observations. Peters and Donoso-Barros (1970) have provided a useful reference, but it is evident that details of geographic distribution are not known for any of the species. Habitat is briefly discussed on the basis of my experience with each species on the study areas, more casual observations made elsewhere, and statements from published literature.

General habits. Behavior under natural conditions, daily schedule of activities, extent of basking habit, reactions to humans or other potential enemies, and food habits are considered. Although much of this material will be familiar to biologists who have done field work where the lizards occur, it cannot be found in the literature.

Growth is discussed mainly on the basis of information obtained by capture, marking, release and recapture. However, only a small percentage of the lizards marked were recaptured and the stunting that resulted from handling and marking hindered understanding of the normal growth rate. Injury, parasitism and disease

also affected growth rates, causing individuals to deviate from the usual pattern. Hatchlings that were marked were rarely captured at intervals suitable to show the amount of growth during the early weeks of life.

In the tropics, discrete age groups are often not evident, and growth rate must be measured directly. Knowledge of growth rate was considered essential to an understanding of population structure and of reproductive cycles. The growth rates implied by the age-size correlations in Table 3 were utilized to calculate approximate dates of birth or hatching and egg laying of individuals and cohorts of young. In every species studied growth rate proved to be variable, and while some young made exceptionally rapid growth, others, perhaps handicapped in ways that were not evident, and destined for early elimination, grew little or not at all in weeks or even months. Only those lizards recaptured after "substantial intervals"—when an area was revisited after a month or more—were useful for study of growth. Even after substantial intervals, some that were already adult when marked showed little or no growth. Others, though marked as young, had attained adult size and stopped growing before recapture. Hence relatively few of the 2294 records of recaptured lizards were of significance in showing growth, and these had to be used selectively.

Spatial relationships were investigated by direct observation on the behavior and movements of individuals, and especially by the recapture of marked lizards, which usually were not at the exact spot of the original capture. The movements involved in travel between points of capture were of various types such as escape dash, normal activity within an established home range, gradual change of home range over an extended period, shift to a new home range, or wandering for any of a variety of reasons. Most lizards probably have home ranges of sorts but these may be ill-defined or ephemeral, and they differ greatly in size, shape, and manner of use according to the habits of the species. One objective of the study was to determine the nature of such areas and to compare them in different species. The essentials of a home range for some kinds are a secure hiding place (or several alternative refuges) to which the animal retreats at any alarm, and a nearby look-out (or several look-outs) from which the lizard awaits its prey. The home range of such an animal is not readily definable because intensity of use decreases rapidly with increasing distance from the activity center, and records are usually concentrated near the center. However, certain other lizards, notably the teiids, are less attached to any particular spot and range more freely over a familiar area in an active search for food. For such species the data are best adapted to calculate home ranges by the method of equating average distance between points of capture with home range radius (Fitch, 1958b:73). If the home range is covered uniformly, individual movements recorded should form a graduated series from zero up to a maximum range diameter, with a few much longer movements representing shifts. (See Figs. 7 and 11.)

Temperature relationships were investigated in many but not all of the species by taking body temperatures and adjacent air temperatures at the time of capture demonstrating a somewhat different level of preference and range of body temperature in each species.

Reproductive cycles are discussed partly on the basis of proportions of adult females that are fecund at different times and the stage of reproduction represented by the gonads of those dissected. Also, the seasonal distribution of hatchlings and older young was taken into account to judge the relative level of reproductive ac-

tivity at different times of year. Lizards that were of hatching size or only a little larger showed by their occurrence and relative abundance approximately when hatching took place. For kinds in which normal incubation period was adequately known, times of egg-laying could be calculated for each hatchling. Knowledge of growth rates permitted similar projections of data to calculate an approximate hatching date and egg-laying date for each partly grown juvenile. Of course, incubation periods and growth rates are subject to fairly wide variation, even in one species at one locality, and the older the individual, the greater the range of error in extrapolating back to the date of hatching and of oviposition. However, the expected margin of error is usually small in terms of the annual cycle. The different approaches sometimes produced somewhat conflicting results, with unconformities resulting from the sources of error mentioned above, and also from inadequate samples.

For the sake of brevity, the following conventions are used throughout: "length" =snout-vent length in millimeters; temperature figures=degrees Centigrade; "KU"=University of Kansas Museum of Natural History.

TABLE 1. Kinds and numbers of field records, and localities, for various species.

Species	Number processed, marked and released	Number of recaptures	Number processed without marking	Number recorded as size estimates without capture	Localities†
Gonatodes albogularis	374	47	37	820	B, BB*, L**, P, PDC, Q, S
Lepidoblepharis xanthostigma			5		B, SM, T
Anolis biscutiger			83		Q*
A. cupreus	2542	820	449		BB*, C, FT, LI**, LP, PDC, Q, S**, SJ**
A. humilis	316	45	128		B**, SM**, T
A. intermedius	284	97	30		C, HEP, SJ*
A. limifrons	980	264	688		B**, P, SM, T**
A. lionotus	37	10	5		SM*, T
A. sericeus			18		BB, LI, PDC, Q, S
A. tropidolepis	428	185	50		HEP**
Basiliscus basiliscus	129	28	56	778	BB, FT**, LI**, LP, Q, S
B. plumifrons	3	1	6		B, C, P, SM
B. vittatus	165	35	9	337	B, P**
Ctenosaura similis	153	13	2	745	BB**, FT**, LI, PDC*, Q*, S
Iguana iguana	4		14	35	BB, FT*, LI, PDC, Q, S
Sceloporus malachiticus	226	19	92	715	C**, HEP, LP, SJ*
S. squamosus			12		PDC, S
S. variabilis	1005	374	10		BB**, FT, LI, PDC**
Gerrhonotus monticola	6				HEP
Ameiva festiva	6	1	7	53	B, P, T
A. quadrilineata	21	4	5	712	P, Q*
A. undulata	160	49	3	251	BB, FT, LI*, LP*, PDC, Q, S*
Cnemidophorus deppii	1117	244	1	704	BB**, PDC**, S
Mabuya mabouya			3		B, P
Scincella cherriei	159	58	29		B, Q, T**

† B=Beverly, BB=Boca de Barranca, C=Cartago, FT=Finca Taboga, HEP=Hacienda El Prado, L=Limón, LI=La Irma, LP=Las Pavas, P=Portéte, PDC=Playas del Coco, Q=Quepos, S=Sardinal, SJ=San José, SM=San Miguel, T=Turrialba.

* Sources of moderate amounts of information.

** Sources of relatively large amounts of information.

Table 2. Sizes* of lizard species studied.

	Largest adult ♂ (or ♀)			Typical adult ♂			Typical adult ♀			Smallest reproductive ♀			Typical hatchling		
Gonatodes albogularis	48	65	2.5	43	56	2.0	42	45	2.2	35.5	39	1.2	18	19	.1
Lepidoblepharis xanthostigma	41	49	(♀)	37	46		38	46		34	41				
Anolis biscutiger	43	83	1.5(♀)	39	80	.99	40	78	1.05	33	63	.8	17	32	.14
	41	84	1.1(♂)												
A. cupreus	52	93	2.5(♂)	47	84	1.8	39	70	1.4	35	60.5	1.0	18	27	.2
A. humilis	44	69	2.2(♂)	38	60	1.3	40	76	1.8	32	62	.7	16	24	.15
A. intermedius	54	85	3.0(♂)	48	77	2.0	47	74	2.1	38	62	.9	18	27	.15
A. limifrons	45	92	2.0(♀)	39	81	1.4	40	81	1.5	33	66	.9	17	33	.14
	43	92	1.7(♂)												
A. lionotus	85	148	(♂)	79	140		69	113		60	100		23	35	
A. sericeus	52	114	2.4(♂)	44	95	1.6	41	84	1.23	36	72				
A. tropidolepis	59	108	4.0(♂)	53	102	3.5	52	84	33	42	67	2.0	20	35	.2
Basiliscus basiliscus	228	565		215	534	250	150	318	93	117	303	45	43	90	1.7
B. plumifrons				194	520					113	326				
B. vittatus	145	420	90	134	387	70	115	314	42	86	237	15	39	87	1.5
Ctenosaura similis	440	800		415	675		335	515		212	382		57	130	
Iguana iguana				530	1237		390	920		316	745		60	253	
Sceloporus malachiticus	90	100	(♂)	83	95		78	85		64	72		29	29	.8
S. squamosus				50	110		49	104					26	54	
S. variabilis	77	121	16.0(♂)	68	107	11.0	63	83	7.0	44	69	3.2	23	32	.45
Gerrhonotus monticola	87	147		82	135		77	123		63	101		26	68	
Ameiva festiva	115	252		104	220		104	210		77	156		37	70	
A. quadrilineata	82	180		72	151		70	140		58	116		30	57	
A. undulata	119	262		107	225		97	194		79	158		35	67	
Cnemidophorus deppii	93	202		78	160	9.0	70	145	7.0	59	133	4.5	31	67	.7
Mabuya brachypoda	91	150	(♀)	63	107		71	117		62	102				
M. mabouya	90	148	(♀)	73	124		82	135		73	120				
Scincella cherriei	63	101	4.8(♀)	54	90	2.5	55	85	2.7	48	73	1.7	22	30	

* SV Length in mm; tail length in mm; weight in gm.

Species Studied or Observed

Thirty-four species were observed during the course of my field work, but eight of them were observed rarely (some only once) and so nothing of note was found out about them. These were *Sphaerodactylus lineolatus* Lichtenstein and von Martens and *Phyllodactylus edwardofischeri* Mertens from Finca Taboga, *Thecadactylus rapicaudus* Houttuyn from Beverly, *Anolis pentaprion* Cope from La Irma, Boca de Barranca and Quepos, *Anolis biporcatus* Wiegmann and *Anolis carpenteri* Echelle, Echelle and Fitch from Turrialba, and *Anolis capito* (Peters) and *Corytophanes cristatus* (Merrem) from San Miguel de Sarapiquí. Twenty-five other species were found frequently and in substantial numbers. A twenty-sixth species, *Mabuya brachypoda*, was seldom found in the field, but is included in the species accounts because museum specimens were available for study. Tables 1-3 summarize respectively field records and localities, sizes, and growth for the 25 species most extensively studied. In Table 1 localities marked with a double asterisk provided relatively large amounts of information, those with a single asterisk contributed moderate amounts of information, and those unmarked contributed relatively little because of local rarity or other conditions preventing an intensive population study.

Family Gekkonidae

The two species of geckos included are

both sphaerodactylines. They attain high population densities and are important predators on small arthropods. These lizards are near the minimum size of terrestrial vertebrates. They are short-legged, dull colored, crepuscular and somewhat secretive. They lay spherical eggs with hard calcareous shells, one at a time. The incubation period is remarkably lengthy and the hatchlings are relatively large.

Gonatodes albogularis (Duméril and Bibron)

Description. Small, short-bodied, with short legs and tail, broad head, large lidless eyes with vertical pupils, body flattened, tail cylindrical, skin velvety with minute granular scales, male black with blue dots on sides, orange-yellow head, conspicuous white and blue markings on labial region, and conspicuous white tail tip; female retains juvenile pattern of pale grayish brown mottled with small, irregular blackish areas (Plate IV, lower left).

Range and habitat. Occurs from El Salvador south through most of Central America and northern half of South America, Cuba, Lesser Antilles and Curaçao. In Costa Rica it is limited to low altitudes near sea level but occurs on both coasts, in warm climates ranging from those of the persistently wet rain forest to those with a long and severe dry season and a xerophytic type of vegetation.

The habitat is on tree trunks. Places of concealment, holes and crevices, are essential. The strangler fig with its tangle of roots above ground level, providing a great abundance of hiding places, is well suited to this gecko's needs; large fig trees often harbor sizable colonies of the lizards, and the local distribution may be in part determined by the availability of fig trees. Many other kinds of trees are utilized however, especially those having rough bark in large, loose flakes, having trunks forked with narrow crevices between them, or having small cavities such as those made by large insects, or those having holes beneath the roots. Man-made struc-

TABLE 3. Typical early growth: lengths of young from hatching to 10 months.

	Hatchling	1 month	2 months	3 months	4 months	5 months	6 months	7 months	8 months	9 months	10 months
Gonatodes albogularis	18	22.7	26.2	29.5	32.6	35.5*	38.2				
Anolis cupreus ♂	18	23	28.5	33.5	38	42	45.5				
♀	18	23	28	32	35*	37.5	39				
A. humilis	16	20.5	25	29	32.5*	35.5	38				
A. intermedius	18	24	29.5	34.5	39*	43	46				
A. limifrons	17	24	29	32.7*	36	38.7	40.2				
A. tropidolepis	20	23.8	26.5	29.1	31.6	34.0	36.3	38.5	40.5	42.3*	43.9
Basiliscus basiliscus	43	59	70	79	87	94	100	105	109	113	117*
B. vittatus	39	52	62	70	76	81	86*	90	94	98	101
Ctenosaura similis	57	69	80	90	100	110	119	128	137	146	155
Sceloporus malachiticus	29	37	44	52	55	60	64*				
S. variabilis ♂	26.5	30.5	36	41.5	45.9	55.3	60				
♀	26.5	30.5	36	41.5	44.4*	47.3	50.2				
Ameiva quadrilineata ♂	30	43	50.4	53.4	56.4	59.4	62				
♀	30	43	48.6	52.0	54.0	56	58*				
Cnemidophorus deppii ♂	31	40	46	54	60	66	72				
♀	31	38.5	43	48	53	58*	62				
Scincella cherriei	22	27	31.5	35.5	39	42	45	48*	51		

* Approximate minimum size of female at sexual maturity.

tures including fence posts, especially those retaining bark but having it warped and separated from the wood beneath, stone walls, concrete foundations of buildings, logs and trash are utilized. In most instances these geckos have been seen between ground level and an elevation of about 4 m.

General habits. This gecko is scansorial, and during periods of activity it darts about, over vertical or inclined surfaces of tree trunks, stalking its insect prey. It is mainly diurnal, but activity is concentrated in late afternoon, beginning about sunset, or considerably earlier when places of foraging are in deep shade. Each individual has its own small area of tree trunk with home ranges or territories of a few square meters at the most. At any sudden movement the shy and furtive geckos dart into holes or crevices and disappear. Usually the dash for shelter is only a few centimeters. If routed from its shelter, the gecko most often runs spirally around the tree trunk to another refuge, and disappears within a second or two. Interactions between individuals are marked by frequent pursuits of the smaller by the larger. Predation of large individuals on small ones seems probable. A tail-waving display by adult males serves as a territorial signal, and probably each adult male controls a definite area and excludes other adult males from it. However, holes and cavities that provide the best retreats are sometimes used by groups of individuals and seem to be communal property.

On the Marbella Hotel grounds at Boca de Barranca trunks of two large tamarind trees were known to harbor six to ten individuals each but in general the population was well dispersed, often with only one or two individuals per tree trunk or fence post. In contrast, at the Limón city park, each of the many large fig trees harbored a sizable colony, perhaps several dozen in some instances. The lizards were so abundant that interactions between them were almost continual at times when they were active. Aggression or escape accounted for much of the activity. In this urban situation the geckos were largely free from natural enemies such as snakes, larger lizards and predatory mammals, resulting in unusually high density and intensified intraspecific competition.

Growth. Fifteen of the geckos that were marked at Boca de Barranca were recaptured after intervals appropriate to show growth. For the 9 best records, gains in length were 20 to 26 in 57 days, 25 to 29 in 49, 28 to 33 in 43, 30 to 38 in 85, 28 to 36 in 57, 33 to 41 in 130, 22 to 33 in 95, 34 to 46.5 in 178, and 33 to 43 in 352. The last in this series was a male and the preceding two were females; all the others were of undetermined sex. Relatively rapid growth is indicated, and at an age of six months young have reached the size of sexual maturity. Age-size correlation is shown in Table 3.

Spatial relationships. For 36 recaptures average distance was 9.3 m, extremes 0 to 55 m (see Fig. 7). In 16 instances the gecko was recaptured at the place it was released, or had moved no more than 3 m (within the distance sometimes covered in an escape dash) and was judged to be in the same home range. Most other recorded movements were from 4.6 to 15.3 m over periods of one to 18 months, usually indicating that the lizard had shifted from its original tree or fence post to another nearby. The four longest movements (not shown in Fig. 7) were 52, 52, 37 and 31 m in intervals of 63, 51, 42 and 50 days, respectively. The three longest movements were made by adult males.

Where conditions are favorable an individual seems to remain permanently in the same area of a few square meters and to use the same shelter. Territorial pressure is probably an important cause of shifts, especially in adult males. An en-

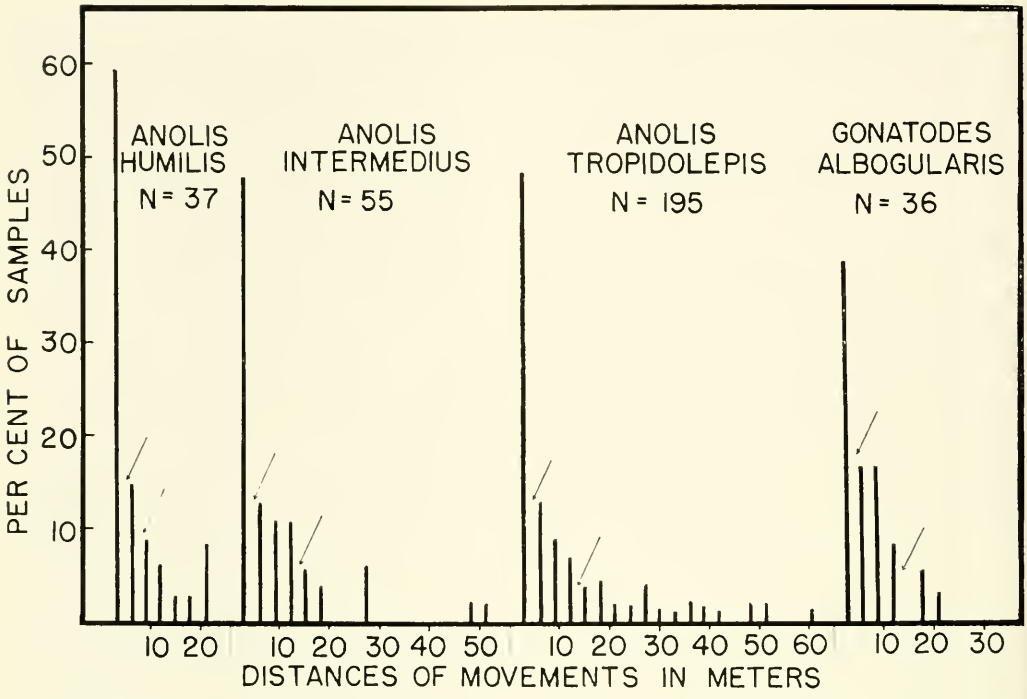

FIG. 7. Distances between points of capture for marked and recaptured lizards of 4 species. Arrows are intended to suggest tentative partial separation of what may be different kinds of movements: short distances within an ordinary home range, medium distances indicating unusually large, elongate, or altered home ranges, and relatively long movements indicating wandering or shift of range.

counter between two adult males, that appeared to involve mutual defense of territories, was observed at Portéte on 30 Aug. 1969. The lizards were on the vertical surface of a rock wall, about 0.4 m apart. Their tails were elevated, and bowed with their tips directed forward over the lizard's backs, and were undulated in a somewhat jerky motion that rendered the white tail-tips extremely conspicuous. From time to time one or the other gecko would rise to an aggressive posture, standing high on its legs, and would sidle jerkily toward the opponent. Heads of both males were lowered, and at times of maximum stress as they came within about 0.3 m, there was a series of peculiar lateral twitching or snapping motions of the heads, which were turned toward the opponents. The confrontation consisted mostly of threat, but once a lizard darted at the other, striking him and perhaps biting him. Each male in turn became the aggressor but with seeming reluctance to move into the area occupied by the rival.

Reproductive cycle. The eggs are white, spherical, hard-shelled and calcareous. Quesnel (1957) found that females of the closely related *G. vittatus* produce eggs at approximately monthly intervals. Eggs of several individuals may accumulate in tree holes and other sheltered places such as those the lizards themselves occupy in periods of inactivity. The incubation period is not precisely known, but judging from the time taken for eggs found in the field to hatch, it is at least four months.

Sexton and Turner (1971) studied a local population of this species at Ancon, Panama Canal Zone, over an entire year and determined the reproductive cycle chiefly on the basis of the numbers of eggs

laid in communal nesting sites over bi-weekly intervals. Ancon is characterized by a dry season, including January through early April, when there is little precipitation, and during this period oviposition almost ceased, but it gradually increased to a peak at the wettest time of year, September and October. Evidence from dissection of females was less clear-cut but tended to bear out the trend of egg collections, as the highest proportion of sexually quiescent females was found in mid-February and greatest numbers of females with oviducal eggs were found in May, June and July. Possibly retention of eggs by females during periods that are unfavorable for laying may alter the results.

In my own study, based primarily upon presence of recently hatched young, and secondarily upon uterine or ovarian eggs or gravid appearance of females, the trend was different. At Limón nine samples averaging 100 lizards each, and well distributed over the year, all included hatchlings and other young up to adolescent size, with no size-group missing from any sample. Obviously egg-laying or at least hatching was continuous throughout the year in this population. The climate of Limón is notably wet, but with relatively little precipitation in February, September and October. The ratio of young to adults did not show well defined seasonal trends in my samples (see Fig. 8). In this urban area growth and reproduction were affected by high population density. Adult size averaged smaller than in other populations and young of all sizes were scarcer. Young up to 32 mm, thought to be in their first four months, were 39.6% of the combined year-round Marbella samples but only 16.9% of the Limón samples. Cannibalism is suspected as a density-dependent mortality factor reducing the numbers of young at Limón.

At Boca de Barranca on the grounds of the Marbella Hotel, ten population samples were obtained by capture-recapture, representing all months except March, September and October. The climate at this locality is comparable to that of Ancon, Canal Zone, with a virtually rainless dry season extending from December into April. Nevertheless, young of hatchling size or but little larger were present in every sample, indicating year-round hatching in this population also. In two August samples young that were less than half grown were poorly represented, indicating (on the basis of an estimated four-months incubation) reduced egg-laying in December, January, February and early March (see Fig. 9). Samples from early January, early and late February and early April had a high proportion of hatchlings and other young, indicating that there is more

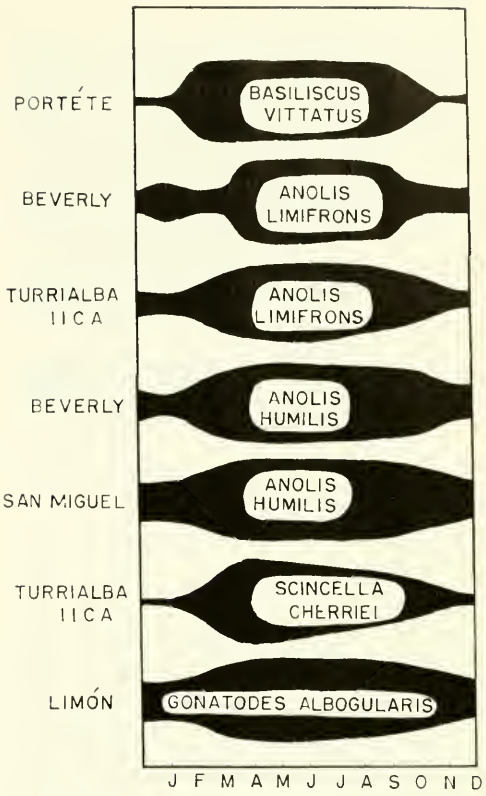

Fig. 8. Relative levels of egg production through the year in 7 lizard populations of the Caribbean versant in areas of high rainfall.

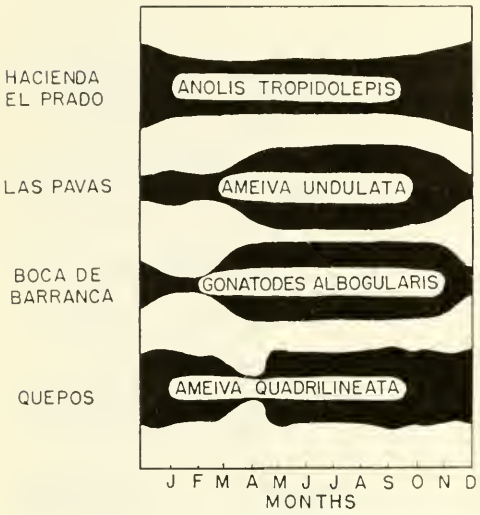

FIG. 9. Relative levels of egg production through the year in 4 lizard populations of the Pacific versant.

egg-laying in September-November than at other times of the year. Females dissected during the dry season invariably had either a large ovarian follicle or a uterine egg. Most of the females obtained were not dissected but were marked and released. When a female had a shelled egg in the oviduct, nearly ready to be laid, it could be discerned through the ventral body wall. In every sample there were some such obviously gravid females.

Lepidoblepharis xanthostigma Noble

Description. Small with short legs and digits, a narrow head, large lidless eyes having round pupils, tail heavy and cylindrical, usually between 1.1 and 1.25 times length; skin velvety with minute granular scales dorsally, and larger, imbricate scales ventrally; color above dark brownish lavender marbled with indistinct lighter areas, and with a pair of white dorsolateral lines distinct in some individuals, faint and/or broken in others, head paler than body; venter light lavender, with brown dots and reticulations on chin; each claw retractile into a compressed sheath.

Range and habitat. Occurs from Nicaragua south through humid lowlands of both Caribbean and Pacific coasts, and at intermediate elevations up to about 1500 m; south to Colombia. Typical habitat is in leaf litter in rain forest, but the species occurs also in altered situations, especially in cacao groves.

General habits. These geckos are secretive and tend to stay out of sight beneath dead leaves even when they are active. Occasionally one flushed by movements of a person is glimpsed darting across an open place.

Reproductive cycle. Like other sphaerodactylines these lay only one egg at a time and the right and left ovaries alternate. Sixty-six specimens (KU) from Costa Rica (mainly north-central part) represent June (8), July (22), August (18) and September (18). Each sample contained gravid females and young of several sizes. The smallest juvenile, collected in July, was 20 in length. If *L. xanthostigma* parallels *Gonatodes albogularis* in incubation and early growth, the gravid females and young of different sizes, found in June, July, August and September, may be construed as indicating egg-laying in every month of the year.

Family **Iguanidae**

This large family is especially well represented in the Neotropical region and includes 16 of the 26 species in the present study. These constitute four phylogenetic and ecologic groupings, anoline, basiliscine, iguanine and sceloporine. The anoles are represented by many species; they are slender, active, mostly small lizards that are primarily arboreal, but with kinds that are secondarily terrestrial (*Anolis humilis*) or even semi-aquatic (*A. lionotus*). Eggs are produced singly with left and right ovaries alternating, sometimes in unbroken sequence when environmental conditions remain favorable. In contrast with many other iguanids, anoles need to drink fre-

quently, are subject to desiccation, and hence tend to be limited to moist situations. The egg is left poorly concealed, or dropped in superficial situations. A notable aspect of anole ecology is widespread sympatry between species with competitive relationships and some degree of habitat partitioning (Schoener, 1968). The species that I studied occurred in various combinations, with two to several at each locality.

The basilisks are medium-sized lizards of riparian habitats, predatory and partly herbivorous. Size differences between young and adults and between adult males and females are unusually great. Growth and longevity are prolonged. The populations studied always consisted mainly of immature individuals.

The iguanines, *Ctenosaura similis* and *Iguana iguana* are notable for their great size, largely herbivorous habits, and clutches of eggs that are near the maximum for lizards. Size difference between young and adults is extreme and attainment of maturity is delayed until the second year or longer.

In the fourth group, the three species of *Sceloporus* are alike in being medium-small, insectivorous heliotherms, but otherwise are ecologically divergent. These are the three southernmost species of the genus, which is widespread in Central America and southern North America. Conforming with a general trend, the montane *S. malachiticus* is viviparous, whereas the two lowland species, *S. squamosus* and *S. variabilis* are oviparous.

Anolis biscutiger Taylor

Description. Small and slender with long limbs (hind reaching anteriorly beyond eye), attenuate tail (about twice length) and head pointed, with frontal concavity; dorsal scales extremely fine and granular, ventrals smooth, two pairs of much enlarged postanal scales; color above, light, yellowish olive, darker in occipital region, ventrally pale, yellowish; obscure dusky bands on legs and toes; some individuals have small median or paired black dorsal spots, widely separated; in some females there is a broad pale middorsal stripe with sharply defined dark edges. Dewlap in male relatively small, whitish with pale yellow at base; absent in female. Adult female slightly larger than male. This species resembles *A. limifrons* in most respects, differing from it only in minutiae of scale characters, color and pattern.

Range and habitat. This little known species was recorded by Taylor (1956:81) from Golfito, Palmar, and near Dominical on the Pacific coast of Costa Rica in southern Puntarenas Province. Williams and Smith (1966) noted two specimens from Julieta, extending the known range 60 km farther northwest along the coast from the Dominical locality. The range is within the tropical humid lowlands of southwestern Costa Rica. I found *A. biscutiger* near Quepos (2.5 km E, 12 Dec. 1967; 1-2 km N, 7 March 1969; 23 and 24 Feb. 1969; 6.5 km NW, 16 Jan. 1968; 10 km NW, 19 June 1968; 0.5-1 km NW Río Cañas, 21 Aug. 1968). It was most numerous along the edge of a recently cleared small field in which beans and corn were growing. The field was bordered by dense thickets and was still littered with logs, stumps and debris, especially along its edges. Elsewhere it was found where there were groves of native trees, often on the trunks among vines and epiphytes, and sometimes on the ground in leaf litter. Also, it was found in small numbers in dense, low herbaceous vegetation in plantations of broad-leafed trees.

General habits. Insofar as observed in the capture of 83 *A. biscutiger* and the unsuccessful pursuit of a comparable additional number, its habits and behavior are like those of *A. limifrons*, which ap-

pears to be a near relative replacing it on the Caribbean versant.

Temperature relationships. On 14 Dec. 1967 and 6 March 1969 a total of 33 body temperatures were obtained from active individuals (Fig. 10). Nearly half of the temperatures were in the interval between 31 and 32 (range 29.3 to 32.5). Air temperatures ranged from 27.3 to 32.6 and were concentrated in the interval between 30 and 31. Body temperature averaged 1.31 degrees above air temperature, and exceeded it in all but one instance. It is noteworthy that body temperatures averaged higher than in the closely related *A. limifrons,* with little overlap.

Reproductive cycle. Samples obtained near Quepos on 12-14 Dec. 1967, 18 Jan. and 1 May 1968, 1 March and 26 Aug. 1969 and 23-24 Feb. 1970 consisted almost entirely of adults and most of the females were gravid, but perhaps egg-laying is suspended or delayed in the dry season. The 26 Aug. sample of 8 included a juvenile of 19 mm and a subadult of 32 mm.

Anolis cupreus Hallowell

Description. Medium-small, long-legged, predominantly brown, with fine granular scales; digital lamellae only moderately developed; tail a little less than twice length; male averages markedly larger than female and differs in having a large dewlap which is amber-orange on

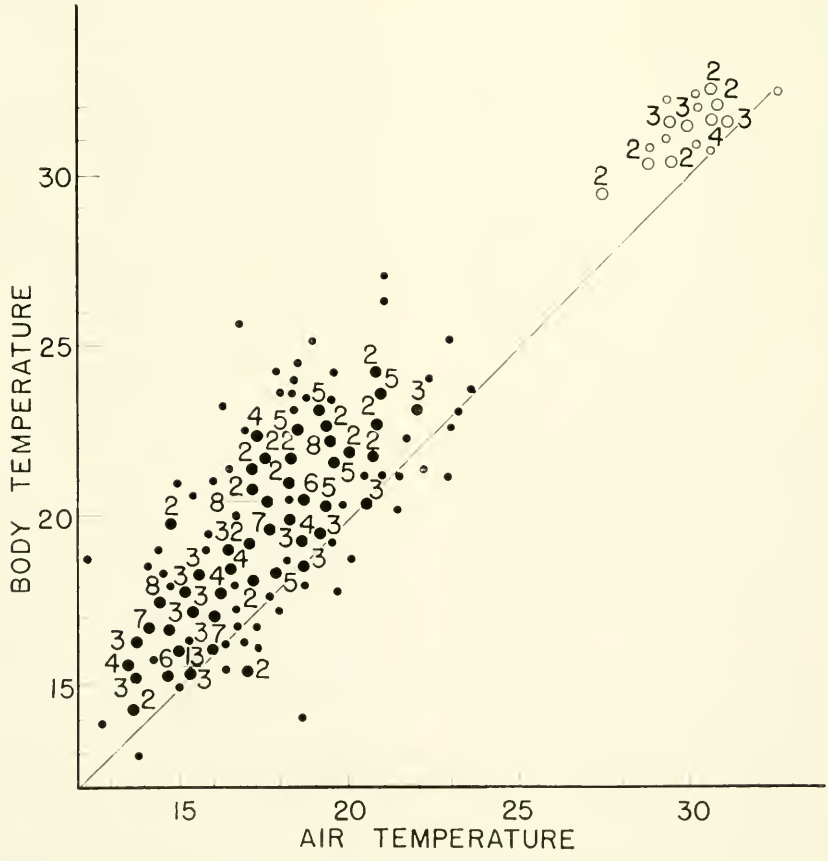

FIG. 10. Body temperatures and adjacent air temperatures of *Anolis biscutiger* (open circles) from Quepos and of *A. tropidolepis* (solid circles) from Hacienda El Prado. Each small circle represents a single record; each large circle represents 2 or more records as indicated by adjacent numbers.

its basal portion and pinkish rose on its outer part. Male often has broad middorsal dirty white stripe bordered by black (Plate IV, lower middle); female pattern usually different and extremely variable, often with a middorsal stripe, which is usually narrower than the male's and may be white, tan, cream-colored or orange, may be reduced to a thin line or may be several scales wide, may be unmarked or may be overlain with a series of chevron-like or diamond-shaped markings; faint, wavy black bars on limbs and tail, variable in shade depending on temperature, light and activity.

Range and habitat. Occurs from Guatemala south into Costa Rica, at low and medium elevations, chiefly on Pacific slope, mainly in northwestern one-fourth of country, east to Cartago and Río Dominical, chiefly in areas having a pronounced dry season. It seems somewhat more tolerant of xeric conditions than are many other anoles.

The habitat is chiefly where there is abundant leaf litter. In the xeric climate of western Guanacaste the species is largely confined to mesic situations along streams where there are large trees and dense shade with leaf litter. The lizards are sometimes fairly common in cafetal, climbing on the coffee trees and utilizing as shelter the brush piles left from the pruning of the trees. They are common along wooden fences or wire fences with wooden posts, especially where there is fairly thick ground vegetation and where the posts are living trees with some foliage, or have some growth of vines or epiphytes. In San José and Cartago large populations have been found in vacant lots, climbing on shrubs, fence posts, buildings or garden walls, or occasionally in thick grass with no objects to climb upon.

General habits. In cool weather it often basks in the sunshine. In hot and dry weather, however, it tends to stay in hiding and ventures out after sunset, foraging even at dusk. Those from higher cooler areas average several degrees cooler body temperature than those in the hot lowlands.

The lizards are partly terrestrial. In the places where they are found, herbaceous vegetation or leaf litter is abundant and one may disappear beneath this shelter in response to danger. Also there are strong climbing tendencies, and a lizard may dash a meter or more to a tree or shrub to escape. On a large tree trunk it usually runs spirally upward. On a shrub, vine or sapling it may ascend keeping the stem between itself and the pursuer, and then crouch, concealed except for its feet which clasp the stem within view.

Populations attain remarkably high densities. Several adults may be found within a square meter, or on the same fence post or tree trunk. The dewlap is especially large in the male and the display is well developed. Presumably there is territoriality of sorts. At San José and Cartago where the lizards were found in large numbers in vacant lots, cafetals and roadsides, males were often conspicuously perched on fence posts which seemed to be territorial look-outs. Search would often reveal a female closely associated with the male, but in a lower much less conspicuous place.

Growth. A total of 820 recaptures of marked *A. cupreus* were recorded, mostly after intervals of several weeks up to 22 months, but many of the lizards were already adults when they were marked, and relatively few represented the early stages of growth. Although numerous hatchlings were marked, only those of 24 mm or more were ever recaptured. High natural mortality, and delicacy of the hatchlings make them difficult to capture without injury and contribute to the difficulty of tracing growth in the early stages.

In 8 recaptured males from San José,

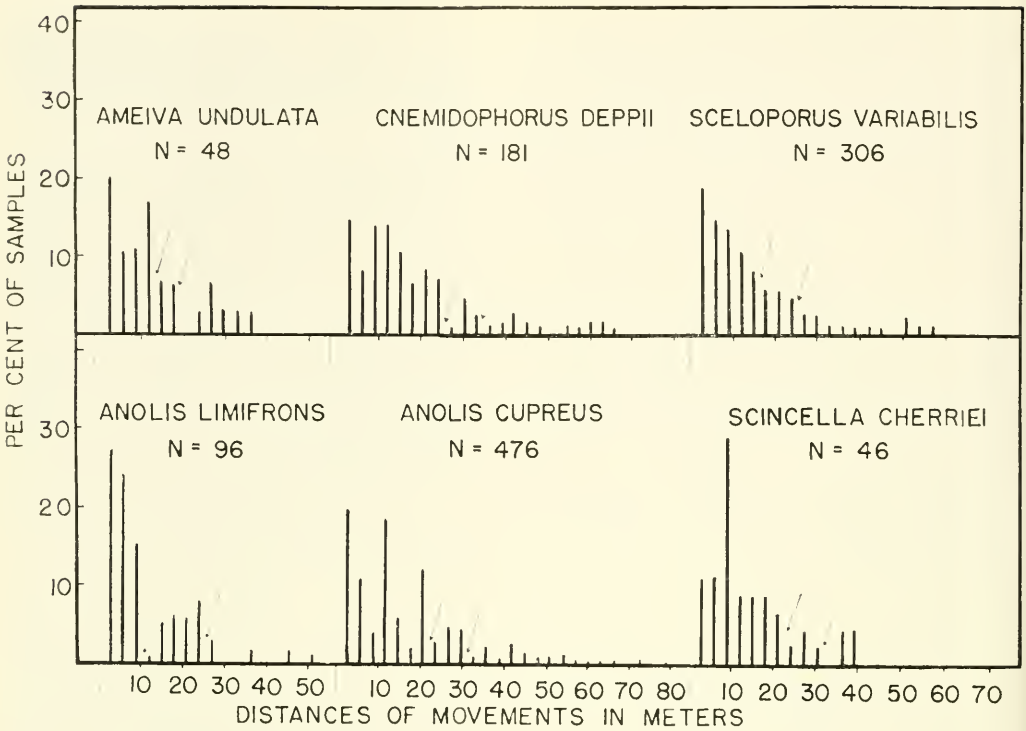

FIG. 11. Distance between points of capture for marked and recaptured lizards of 6 species; arrows as in Figure 7.

Sardinal, and Boca de Barranca, gains in length were 25 to 31 in 17 days, 26 to 36 in 52, 26 to 35 in 89, 24 to 35 in 49, 28 to 35 in 49, 24 to 46 in 200, 27 to 48 in 189, and 33 to 45 to 48 in 267 and 35. In 6 recaptured females from Sardinal and Boca de Barranca gains in length were 25 to 33 to 43 in 49 and 192, 24 to 45 in 41, 28 to 33 to 42 in 12 and 87, 24 to 43 in 150, 25 to 45 in 200 and 29 to 37 in 91. Age-size correlation is shown in Table 3.

Spatial relationships. Compared with the other species of anoles that were studied *A. cupreus* was more vagile, doubtless because of its more terrestrial habits. The longest movement recorded was 210 m and seven others exceeded 100 m (not shown in Fig. 11). However, these were exceptional. As shown in Figure 11, the majority of movements were less than 12 m and nearly one-third of the movements were in the range 12 to 30 m. Inasmuch as the pooled sample of 476 movements includes adults of both sexes and young, from contrasting types of habitats, it could be expected that some individuals would have home ranges much larger than others. Field observations over relatively short periods suggest that in its routine activities an anole of this species normally stays within an area smaller than 12 m across, perching consistently on the same tree or fence post, or staying within a few meters of it when on the ground.

Temperature relationships. Body temperatures of active *A. cupreus* ranged from 18.8 to 34.2, with a continuum between these extremes and no concentration of records that would indicate a preferendum. Air temperatures ranged from 18.4 to 33.6. Maximum body temperatures were recorded in the relatively hot climates of Boca de Barranca and Sardinal (Fig. 12), and La Irma, and at these localities body

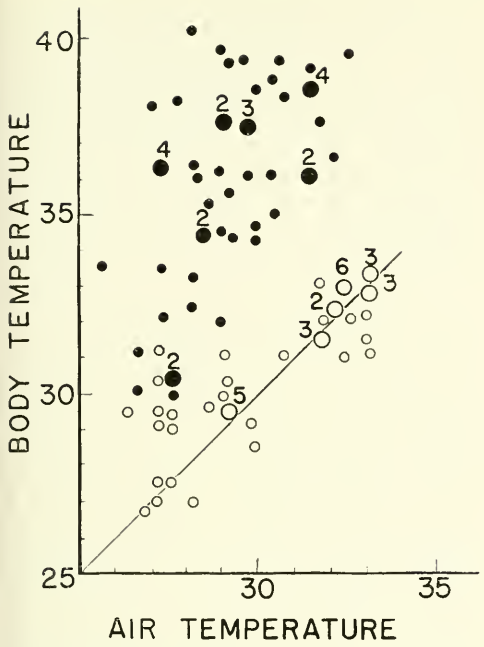

Fig. 12. Body temperatures and adjacent air temperatures of *Ctenosaura similis* (solid circles) from Playas del Coco, Sardinal, and Boca de Barranca and of *Anolis cupreus* (open circles) from Sardinal and Boca de Barranca. Small and large circles show numbers as in Figure 10.

temperatures always approximated the air temperatures of the shaded places where the lizards tended to stay. In the cooler climate at San José the anoles were often observed basking, and their body temperatures were usually higher than air temperatures. However, body temperatures at San José averaged consistently lower than those at lowland localities in warmer climates.

Reproductive cycle. The four populations that were intensively studied all conformed to essentially the same pattern (Fig. 13) with egg-laying extending over about half the year, late April or May through October, and little or no reproduction in the remaining months. The nonreproductive period extends over the entire dry season, which is severe throughout the range of *A. cupreus*; also it includes the beginning and end of the rainy season. At the beginning of the breeding season in late spring the population consists essentially of adults with a few adolescents or large young resulting from late hatch or retarded development. A small percentage of the adults are second-year breeders, but most are still in their first year and still growing. Average adult size increases during the rainy season. Females produce eggs at frequent intervals; for instance, one kept in confinement laid 7 eggs from 15 June to 23 Aug. Intervals between oviposition averaged 10 days but were variable. In some instances the interval was not observed because the egg, well concealed beneath debris in the bottom of the container, was undetected for several days. If the production rate of this female was typical, a female surviving an entire

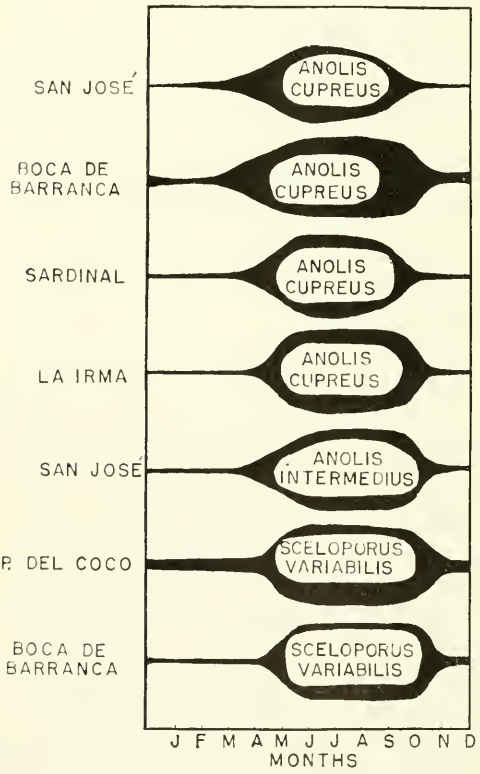

Fig. 13. Relative levels of egg production through the year in 7 lizard populations of the Pacific versant, all in areas having a severe dry season.

breeding season might be expected to produce a quota of at least 18 eggs.

San José has a cooler climate than the other three localities, and collections made in early November and early December are almost lacking in juveniles near hatchling size, but have increasing numbers that are of second-month, third-month and fourth-month size. This distribution seems to show that the season of oviposition was tapering off rapidly in September and October. At Boca de Barranca an early January sample had a few hatchlings indicating that egg-laying had continued well into November. Winter samples from La Irma and Sardinal had young indicating continued egg-laying into early November and late October, respectively. At La Irma and Sardinal hatchlings were appearing in early July, and there were no older young. At San José and Boca de Barranca mid- and late-August samples had young from hatchlings to third month size, indicating that egg-laying began about the same time as at Sardinal.

Many females from various localities, dissected in February and early March, had well-developed fat bodies but their ova were minute. However, in late March and April many of them appeared to be gravid and some of those dissected were oviger-ous. The fact that they were carrying eggs many weeks before actual oviposition occurs, probably means that the fertilized eggs are retained in the oviducts, with development arrested, until environmental conditions favor their deposition.

At Quepos, samples totaling 98 were obtained in December, January, February, March, April and August. The late August sample consisted largely of immatures of graded sizes. The December sample consisted of adults and young that were mostly well-grown, but the smallest was only 24 mm—about 1 month old. The March sample consisted of adults exclusively, and so did the February sample except for one lizard of two-months-old size (28 mm). Thus the seasonal schedule conformed well with that found elsewhere. On 11 March 1970 a series of 78 was collected at Cartago. This series too consisted essentially of adults with the smallest lizard (32 mm) ostensibly representing an egg hatched in late October or early November.

Anolis humilis (Peters)

Description. Diminutive, stout-bodied, relatively short-legged, having 8 or 10 much enlarged rows of keeled dorsal scales; digital lamellae only weakly developed; lateral scales granular; caudal scales large, keeled; color dark, dull brownish olive, sometimes without much pattern and sometimes with a series of connected hourglass-shaped darker brown middorsal marks; a broad V-shaped band across forehead; tail approximately 1.5 times length (often a little longer than this in males and a little shorter in females); dewlap large, deep red with bright yellow outer margin in male, scarcely developed in female.

Range and habitat. Occurs from lowlands of Chiapas, México, south and east through much of Central America, at least through the Canal Zone to eastern Panamá. In general it is confined to low altitudes and warm humid climates and occurs in Costa Rica mainly on the Caribbean slope, but encroaches into parts of Guanacaste and Puntarenas provinces in the Pacific versant.

The habitat is chiefly in tropical rainforest. Often the lizards are in leaf litter, but their abundance centers about the buttressed roots of large forest trees. A colony of a dozen or more may live about a single tree. Where isolated groves or even isolated trees remain, there are often colonies of the lizards. Most that I observed were in cacao plantations where there were occasional large forest trees remaining.

General habits. Activity is strictly diurnal but is in dim light beneath a dense foliage canopy and often under overcast skies or in rain. The radiating buttressed roots of large trees provide surface areas and travelways on which the lizards run, spending much of their time above ground level. Sometimes they have been found more than one meter above ground, but usually they are nearer ground level. They dart rather rapidly over the root buttresses and tree trunks and are not readily distinguished from the geckos that live in the same situations. When alarmed the anoles run in short spurts, often for only a few centimeters, and crouch in sheltered places concealed by low vegetation or ground litter. In the dim light of the habitat they are difficult to see, and after running briefly and stopping suddenly, one may be overlooked and escape.

The large and conspicuously colored dewlap functions in aggressive display. Evidence of territoriality was observed on various occasions when a lizard escaping from me came close to another and elicited the display, but actual combat was not observed. Those that were recaptured after the longest intervals were still at approximately the same spots on buttressed roots.

Growth. Of 35 marked and recaptured after intervals of weeks or months, 20 had made substantial growth. Ten of these are considered most representative. For the 3 males gains in length were 24 to 29 in 44 days, 29 to 36 in 123, and 33 to 38 in 82. For the 7 females gains in length were 18 to 31 in 106 days, 23 to 37 in 118, 28 to 38 in 82, 27 to 40 in 218, 29 to 34 in 46, 34 to 38 in 82, and 37 to 41 in 123. Age-size correlation is shown in Table 3.

Spatial relationships. Anolis humilis was the least vagile of all the species studied (Fig. 7); most of those recaptured were within a few meters of the original site—often on the same tree trunk or root buttress, even after several months.

Temperature relationships. Eighteen body temperatures were obtained, on four different dates at Beverly and San Miguel. All were in the range 20.0 to 26.9 (Fig. 14). In most instances the body temperature was within one degree of the air temperature and greatest deviation was 1.6. Obviously these lizards are non-baskers as sunlight is scarce in their forest habitat. Body temperature is controlled by a combination of substrate temperature and air temperature. Although the records are too few and too variable to indicate a preferendum, it is obviously somewhere in the range 22 to 27 degrees that encompassed most of the records, remarkably low for a tropical lizard and for an anole. Most species of *Anolis* that have been studied have preferenda in the range of 27 to 33 (Ruibal, 1961; Jennsen, 1970; Ballinger, Marion and Sexton, 1971).

Reproductive cycle. Nearly all adult females appeared to be gravid regardless of time of year. Seventy-seven were dissected, and all were found to be carrying eggs. Of these gravid females 47.5% had a uterine egg on each side; 29.5% had a

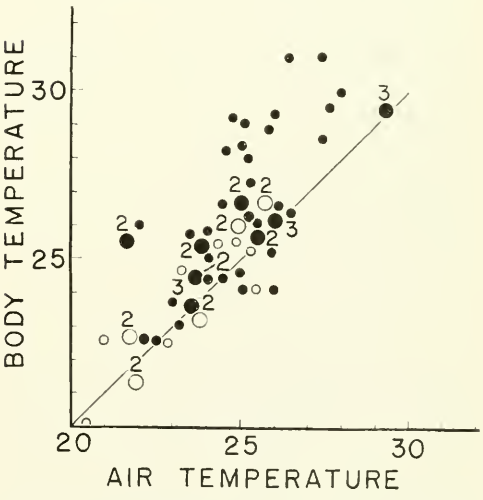

Fig. 14. Body temperatures and adjacent air temperatures of *Scincella cherriei* (solid circles) and *Anolis humilis* (open circles) from Beverly. Small and large circles show numbers as in Figure 10.

uterine egg on one side and a large ovarian follicle on the other; 9.0% had an enlarged follicle on one side only; 7.6% had enlarged follicles on both sides; 6.4% had a uterine egg on one side but no enlarged follicles. In the January-February sample of 13 gravid females 8% had two uterine eggs, as contrasted with 56% (of 25) in March, 57% (of 21) in June, and 44% (of 18) in July-August. No samples are available for the months of September through December.

Evidence of year-round breeding, but with seasonally changing levels, was provided by the distribution of hatchlings and other young. In the 15 population samples from Beverly and San Miguel there were young representing hatching in every month of the year. There were substantial numbers of hatchlings in each sample. Young judged to be less than three months old made up 36.4% of the combined samples. Numbers of hatchlings were relatively low in most January to April samples, bearing out the evidence from gravid females that the rate of reproduction is somewhat slackened during the early months of the calendar year (Fig. 8).

In 12 of the gravid females that had an ovum in each oviduct, the two eggs appeared approximately equal in size, but in the other 25, one egg was definitely larger. Presumably the interval between successive eggs is variable but usually short. A gravid female captured at Beverly on 30 Aug. 1969, laid two eggs overnight, both of normal appearance.

Anolis intermedius Peters

Description. Small, pale greenish olive, somewhat flattened, having medium-short limbs (hind, adpressed, reaches to midneck), toes expanded distally to broad lamellae, ventral scales keeled, tail relatively short and blunt-tipped (usually 1.5-1.7 times length); four pairs of large brownish dorsal spots often discernible, sometimes prominent, on body. Some females have broad, cream-colored or occasionally orange dorsal band with dark edges, but many lack it and are similar to males in color and pattern; dewlap dull white in male, lacking in female.

Range and habitat. Occurs from Nicaragua across Costa Rica to Panamá, at middle and high altitudes, on both Pacific and Caribbean slopes. Upper and lower limits not precisely known, but main abundance is between 1200 and 1800 m. Found on Continental Divide between Cartago and San José; abundant in and near San José, but mainly about eastern part of the city. Not found in the western part of the city nor in nearby suburbs of Escazú and Las Pavas; evidently it drops out or becomes rare as the climate rapidly becomes warmer and dryer to the west.

Trees or large bushes provide the essential part of the habitat. Arborescent plants with small leaves and a thick tangle of stems, preferably thorny, provide a type of habitat that the lizards often frequent. Sometimes massive trunks of large trees are used, especially when there are epiphytes offering effective concealment. Yucca, planted in rows along borders of lawns, roads or property boundaries, are common in central Costa Rica and are especially favored.

General habits. A. intermedius is essentially arboreal. Most of my records are of individuals climbing between 0.3 and 2 m above the ground, but occasionally those pursued have climbed much higher in trees, and also at times they have been seen moving about on the terminal twigs or even the foliage of trees. Several may occur together within a space of a few square meters. Territoriality, if it exists, is of a primitive sort with no rigidly defended boundaries, but with extensive overlapping, and perhaps subordinate individuals are tolerated in the areas de-

fended by those that are dominant. *A. intermedius* has a stereotyped, well-developed display involving spreading the dewlap, but the dull whitish dewlap is far less conspicuous than those of most other species.

A. intermedius is less swift and active than some other species, but it is an accomplished climber. When disturbed, one may dart around to the opposite side of a post or tree trunk, and in doing so tends to move higher, but it may move downward if there is thick cover at or near ground level. In San José and vicinity, where most observations on this species were made *A. intermedius* gave the impression of having much more effective cryptic coloration than *A. cupreus*. When slightly disturbed the lizards have the habit of crouching, flattened against the substrate, and usually their dull surface with grayish or brownish colors renders them inconspicuous. Having climbed as high as possible on a shrub or small tree and still not escaped pursuit, the lizard may turn and run down again to seek concealment on the ground. One that is closely pursued as it climbs often will make a flying leap to the ground and attempt to conceal itself in low vegetation there.

Growth. Marked *A. intermedius* were recaptured from one to five times after substantial intervals, and 32 had made some growth. Most of them represent the middle and late stages of growth, and only one represents the first few weeks after hatching. In 10 recaptured at San José gains in length were 27 to 35 in 45 days, 21 to 26 in 43, 32 to 36 in 42, 32 to 43 in 117, 35 to 44 in 53, 35 to 39 to 46 in 32 and 88, 29 to 44 in 95, 33 to 45 to 48 in 53 and 35, 37 to 48 to 50 in 53 and 29, and 45 to 52 in 86. The first in this series was of undetermined sex, the last four were males and the others were females. Most growth periods overlapped both dry season and rainy season. Tentative age-size correlation is shown in Table 3.

Spatial relationships. Fifty-five recaptures, after an average interval of 45 days, showed movements up to a maximum of 50 m (Fig. 7). Movements averaged 9.5 m. Half were less than 6 m and only two exceeded 27 m. Observations on individuals indicate that one often remains in the same small tree for days at a time, using it as a temporary home range, but that eventually it may shift to another tree or shrub and may occupy a series of them in succession. Nine lizards moved distances of 19 to 27 m to shift from one favorable habitat feature to another. An *A. intermedius* that is well established in favorable habitat probably ranges only a few meters at most from its activity center.

Temperature relationships. Body temperatures ranged from 17.4 to 33.7, but with a preferendum between 25 and 28. Most of the records were obtained from the vicinity of San José (Fig. 15). Fifteen records were from the relatively cool climate in the vicinity of Hacienda El Prado and Vara Blanca on the Continental Divide. These latter records conformed with the general trend of the San José records except that three of them (17.4, 18.2, 18.5) were lower than any in that series. In every instance the recorded body temperature was higher than air temperature; in several instances the difference was less than one degree, but differences of one to three degrees were most common. Air temperatures at which anoles were found active ranged from 15.2 to 28.1, with not much overlap between the two main areas (15.2 to 20.1 for Vara Blanca, 18.4 to 28.1 for San José). Most records were in the range 19 to 26.

Reproductive cycle. Samples were obtained from San José in every month except July and October, and each sample had some females that were obviously

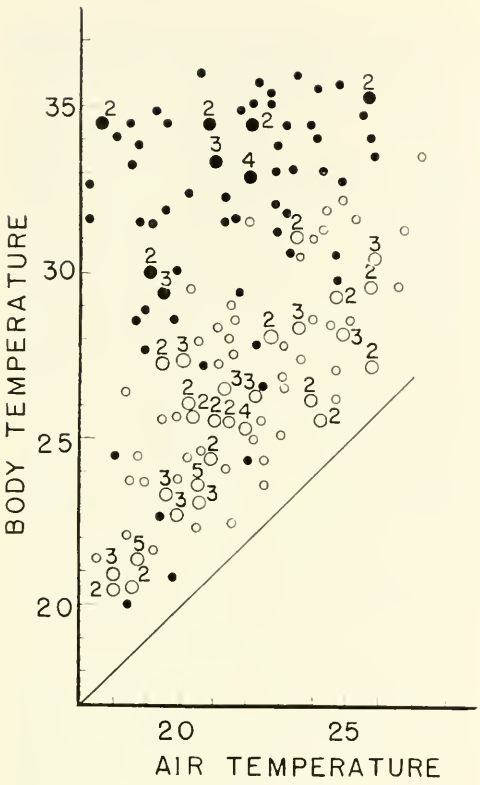

FIG. 15. Body temperatures and adjacent air temperatures of *Sceloporus malachiticus* (solid circles) from San José and Cartago and of *Anolis intermedius* (open circles) from San José. Small and large circles show numbers as in Figure 10.

gravid. Relatively few were gravid in November, but the ratio increased slowly from December to March—a period corresponding with the end of the rainy season and the dry season. The small samples from April, May and June, and better samples from August and September show that most adult females were gravid in this period, whereas in samples taken during the opposite half of the year about half the females were nongravid.

A sample of 91 from early December 1967 had a high proportion of small adults and young of all sizes down to hatchlings, indicating reproduction through the summer and fall months. Samples from 17 Jan. through 7 Feb. 1968 (67), and 18 to 31 Jan. 1969 (77) were similar to each other and combined had only one first-month juvenile, 11 second-month young and 21 third-month young—showing that egg-laying was at a high level in September, but was reduced in October and ended in November. February-March samples are available for 1968 (34), 1969 (44) and 1970 (51). The last was notable for having one hatchling and several second-month young, but in each sample the population consisted chiefly of adults and well-grown young, showing that there was little egg-laying in December and January. April-May (20) and June (33) samples in 1968 consisted entirely of adults (except for one 34 mm male on 11 May), showing that the pause in egg-laying continued through February, March and April. A 10-12 Aug. sample of 19 consisted mostly of medium-large adults, but with young of 22, 24 and 32 mm indicating that a new breeding season had begun, perhaps as early as the end of April. In a 5 Sept. sample half were juveniles, from 18 to 33 mm, showing reproduction from early May through the summer.

The combined evidence from the seasonal distribution of gravid females and young indicates that egg-laying begins in April (or early May) and continues at a high level through October, then dwindles to a stop (or a low level) in November (Fig. 13). Presence of uterine eggs in some females during the dry season is difficult to explain. It may indicate that: 1) eggs are sometimes retained for long periods until conditions become favorable for ovipositing, 2) eggs are laid regularly in the dry season but usually fail to develop due to desiccation, or 3) production of eggs continues year-round but is much slowed in the dry season.

The only clue concerning productivity of individuals was provided by a female captured at San José on 7 March 1970 and brought back to Lawrence, Kansas. She laid an egg on 29 March, and died on 15

April with a fully developed, shelled egg in one oviduct. If she had not died, the interval between ovipositions probably would have been about 17 days. At this rate a female might produce 10 to 12 eggs in the six-months annual breeding season. On 11 March 1970, 16 *A. intermedius* were collected at Cartago, all adults, indicating that here also reproduction was curtailed in the dry season. The many field trips to Hacienda El Prado over a 30-month period resulted in only 18 records of *A. intermedius* and none was below adolescent size, so nothing was learned about the reproductive cycle at high altitude. Presumably incubation and growth are greatly retarded by the low temperatures prevailing at Hacienda El Prado.

Anolis limifrons (Cope)

Description. Small, extremely slender with tail round and attenuate, from a little less than twice to 2.25 times length, head pointed, with frontal concavity; limbs long and slender, the hind, adpressed to body, reaches anteriorly beyond eye; scales minute and granular, those of ventral surface usually keeled; color pale olive above, white with yellowish suffusion below, supralabial region whitish; dorsal black marks usually present but variable, sometimes as several scattered middorsal dots and sometimes paired, or, in female, those on each side more or less fused to form a continuous stripe bordering a broader middorsal cream-colored stripe; male dewlap small and dull-colored, whitish, with a yellow suffusion at its base, dewlap lacking in female; tail with a series of sometimes faint dark rings (better developed in male) separated by wider interspaces; limbs and toes with faint dusky and light bars; females average a little larger than males.

Range and habitat. Occurs from Isthmus of Tehuantepec in México southward through Central America beyond Panama Canal; mainly in tropical zone, but also ascends through subtropical, at elevations at least to 650 m. It is most abundant in humid climates but penetrates into some having pronounced dry seasons.

The habitat is in tropical rain forest, but especially forest edge and disturbed situations including plantations, gardens, thickets, groves, and vine tangles. Often the lizards are abundant in cacao groves. They have been found in coastal coconut groves, but only in small numbers as cover is usually inadequate.

General habits. A. limifrons attains a higher population density than any of the other species investigated. It is both terrestrial and scansorial. Slender build and long legs render it a swift and skillful climber, but much time is spent foraging on the ground, sometimes away from any elevated objects. Sometimes they have been found in meadows, foraging in grass and low herbaceous vegetation. In moving about, they sometimes kept above the mat of low vegetation, and sometimes passed through or beneath it. When pursued, they would progress rapidly with a series of froglike hops. The lizard might conceal itself in dense low vegetation, but generally preferred to climb. One flushed might run rapidly up the stem of a shrub or vine for a meter or two, and then spin around facing downward, and flatten against the stem to conceal itself. At a further alarm it might run back down the stem and either hide in ground litter or dash to another shrub or tree trunk. In climbing the lizards are able to run over leaf surfaces.

Growth. A total of 264 recaptures were recorded at Turrialba and Beverly, but relatively few of these constitute significant records of growth, because most had been marked as adults or subadults. In the following records of the 17 individuals considered most representative of normal growth, "B" designates those from the Beverly study area; all others were from

Turrialba. In 6 males gains in length were 20 to 41 in 224 days (B), 21 to 35 in 88 (B), 23 to 37 in 40, 28 to 38 in 82 (B), 30 to 42 in 77, and 31 to 36 in 36 (B). In 11 females gains in length were 17 to 30 to 33 in 77 and 50 days, 17 to 31 in 75, 22 to 35 in 75, 22 to 35 in 79, 26 to 37 in 76, 27 to 38 in 77, 28 to 41 in 54 (B), 28 to 38 to 41 in 52 and 89 (B), 30 to 33 to 37 in 41 and 41, 31 to 40 in 114, and 33 to 39 to 43 in 77 and 40. The first female listed reached breeding size in a little less than four months from the original capture as a hatchling, but five or six months seem to be more typical intervals for attainment of adult size. Differences in growth rate are not evident between males and females, nor between the population in the tropical climate of Beverly and that in the subtropical climate of Turrialba. Age-size correlation is suggested in Table 3.

Spatial relationships. Records of 96 that were marked and recaptured are available to show movements (Fig. 11). Movements in the neighborhood of 3 to 6 m were most common and the relatively few movements exceeding 24 m probably represent shifts into new areas. The sexes seem to be similar in size of home range and in extent of vagility.

Although objects to climb such as trees, shrubs, fence posts, or vines are important in the ecology of *A. limifrons,* one may have a range which encompasses several climbable objects, and may spend much time on the ground between them.

Temperature relationships. One hundred and twenty-four body temperatures were obtained at Turrialba and Beverly (Fig. 16). Records were concentrated in the range from 25 to 28 which is assumed to approximate the preferendum. In only

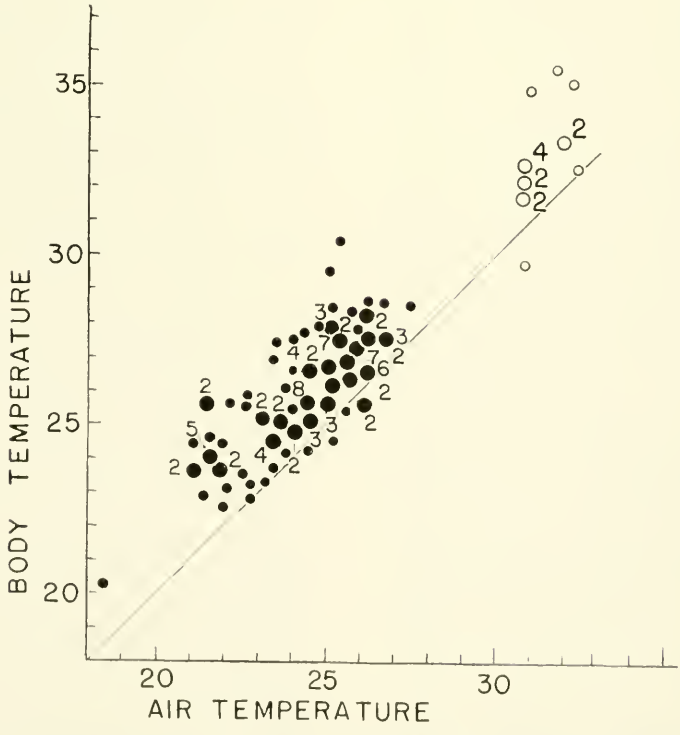

FIG. 16. Body temperatures and adjacent air temperatures of *Anolis sericeus* (open circles) from southern México and Guatemala and of *Anolis limifrons* (solid circles) from Turrialba and Beverly. Small and large circles show numbers as in Figure 10.

five instances was body temperature lower than air temperature, and in each of these the difference was less than one degree. In all other cases body temperature was the higher, but usually it was within three degrees of air temperature.

A. limifrons is often exposed to sunshine during the course of its routine activities, but it is not a persistent basker and usually tends to approximate ecritic temperatures. In the warm, moist climate of its preferred habitat, temperature is usually within or near its preferred range so there is little need for behavioral thermoregulation.

Reproductive cycle. A total of 150 adult females (90 from Beverly and Portéte, 60 from Turrialba) in 16 different samples were dissected, and in each sample the majority of females (79.1%) had a uterine ovum on one or both sides. These females represented the months January through April, June, and August. Six different reproductive categories were recognizable, as follows: 1) uterine eggs on one side and enlarging ovarian follicle on opposite side (57.4%), 2) egg in each oviduct (16.0%), 3) enlarged follicle on one side only (7.9%), 4) nonreproductive (6.0%), 5) ovarian follicle on each side (5.3%), 6) egg in one oviduct (7.4%). The changing ratios of these categories showed no clear-cut trends from one sampling period to another, or between the localities. In three instances (in early March and late August) a large female with two uterine eggs had also an enlarged ovarian follicle on the same side as the more advanced ovum. The simultaneous occurrence of three reproductive units in the oviducts and ovaries might indicate accelerated reproduction with shortening of the interval between oviposition, or it might indicate merely a retention of an egg ready to be laid, with concurrent development of a new follicle. Alternation in ovulations by the left and right ovaries is indicated by the fact that the majority of females had an enlarged follicle on one side and a uterine egg on the other, or if both oviducts contained eggs, these were often of different sizes. The more advanced egg might be already shelled, but a female never contained two shelled eggs simultaneously. Relative bulk of the larger and smaller eggs varied widely between individuals, indicating that intervals between ovipositions are highly variable. Perhaps the rate of maturation of eggs changes also, according to weather, food supply or other factors. Evidence from the females dissected and from a much larger number examined and released indicates that reproduction is continuous throughout the year.

The changing ratios of hatchlings and other young in the population provides a basis for judging the seasonal distribution of ovipositions. At Beverly hatchlings varied from 41% of the October 1967 sample to less than 1% of the March 1970 sample. The high ratio of young up to 26 mm long in the October sample indicates peak production in August and early September. Abundant young up to 32 mm in late August and early September samples also indicate high production from late April to early July. In five March to June samples the ratios of young are lower, indicating some slackening of the rate of reproduction from mid-January to early May.

At Turrialba the population samples showed a similar seasonal trend with high ratios of young in June, August and especially November, indicating reproduction at a high level from mid-March through October, and with much fewer young in January through April samples indicating a reduction in rate of reproduction from December into early March (Fig. 8). The sample size varied from 46 to 218 and averaged 116, but much larger samples would be necessary to measure precisely the frequency of occurrence of any given

age class. Anyhow, the ratios of hatchlings and of other young varied unpredictably. For instance, within the period 20 Feb. to 18 March in three different years percentages of hatchlings in samples at Turrialba were 18.4, 7.6 and 2.3% and at Beverly were 14.4, 7.1 and 0.7%. Varying weather and changes in local habitat from year to year are thought to be more important than small sample size in causing such variation.

Sexton et al. (1971) observed year-round changes in the reproductive organs of male and female *A. limifrons* at several localities in the Isthmus of Panamá. Five localities were near the Pacific end of the Panama Canal, where annual precipitation averaged 1779 mm, two were near mid-Isthmus where precipitation averaged 2729 mm, and two were near the Caribbean end of the Canal where precipitation averaged 3140 mm. All localities had much reduced precipitation from about mid-December to about mid-April but drought was much less severe on the Caribbean side and at mid-Isthmus than on the Pacific side. The authors found that in the dry season reproduction is virtually at a standstill on the Pacific side (most females lacking enlarged follicles and oviducal eggs) and is somewhat reduced at mid-Isthmus and the Caribbean side. In males, testis weight decreased during the dry season but mature spermatozoa were always present. It should be noted that Isthmian *A. limifrons,* compared with the Costa Rican populations studied by me, are larger, have larger more highly colored dewlaps, and are perhaps subspecifically or even specifically distinct.

Anolis lionotus (Cope)

Description. Medium large, semi-aquatic, having elongate body and tail and medium limbs (hind extends forward about to level of eye) and relatively short muzzle; about 20 rows of enlarged dorsal scales, some slightly keeled; ventrals enlarged and heavily keeled; postanal scales somewhat enlarged; tail slightly compressed; dorsal color olive with faint dusky bands on body, limbs, and toes, and black, white-edged bands on the tail; a pair of cream-colored lateral stripes arising behind eye on each side and passing through ear, above front leg back to groin, bordered by darker olive areas; under surface cream-colored with yellowish (or in some adult males, salmon-colored) suffusion; dewlap in male large, light orange; lacking in female.

Range and habitat. Occurs from Chontales, Nicaragua through much of Costa Rica, and at least to Cocuyas de Veragua, Panamá. In Costa Rica it occurs in the tropical and subtropical zones chiefly at medium-low elevations, but perhaps is not widespread on the coastal plain, preferring swift mountain streams. It was usually found perched on a rock in a stream, or else in the relatively barren rocky riparian zone below high water mark. Occasionally, individuals were seen in dense vegetation but always within a meter or two of the edge of the water.

General habits. This anole is partly aquatic and spends nearly all its time at the edge of the water. The dark color and immobile stance cause the lizard to blend with the surroundings so it is not highly conspicuous. It enters the water without hesitation, and swims and dives easily. Upon approach of a person the lizard usually flushes at a distance of several meters, and moves towards a more sheltered place. Usually the dash is short (often less than 1 m) and the lizard runs over rocks on shore and through the water indiscriminately. It may run to a crevice beneath or between boulders, or beneath undercut tree roots, it may dive and hide beneath a submerged flat rock, or it may plunge into the rushing water, and be swept downstream. However, in such cases the lizard

swims vigorously underwater, gains the lee side of a boulder before travelling far, and hides submerged or with only its head protruding.

Growth. From 2 March to 16 April 1968 a young male grew from 39 to 40 mm and another young male grew from 36 to 43 mm. Presumably there was some stunting in both, especially in the first. Maintaining a relatively low body temperature, *A. lionotus* may grow less rapidly than most other anoles.

Temperature relationships. Six body temperatures obtained in the field ranged from 19.2 to 26.2; the lowest one was slightly lower than ambient air temperature, but all the others were slightly higher than air temperature.

Campbell (1971) obtained 13 body temperatures of *A. lionotus* in Panamá, which averaged 26.4 (range: 26.0-26.8). He concluded that both this species and the similar *A. poecilopus* are heliophobic, since over 600 hours of observation failed to produce any records of basking behavior or voluntary exposure to high light intensities. In a laboratory temperature gradient anoles of both species spent most of their time between 26.1 and 28.0.

Reproductive cycle. One female was captured in 1968 on 10 Jan., 1 March, 16 April and 1 June, and was obviously gravid on each of these dates. At least one oviposition might have occurred in each interval, and the four captures span nearly half an annual cycle, suggesting continuous egg production during these 5 months. The lizard was only 60 mm long, minimum reproductive size, on 10 Jan. but had grown to 66 mm, still less than average adult size, on 1 June. A second female was also gravid on 10 Jan. and again on 17 Aug. She was preserved on the latter date and had a fully developed egg 11 x 5 mm in the left oviduct and a follicle 5 mm in diameter in the right ovary. Another female caught on 10 Jan., one on 16 April and one on 17 Aug. were also gravid. Gravid females from Costa Rica (KU) include: 10 from January, 1 from June, and 6 from July. All females longer than 63 mm were found to be gravid.

The gravid condition of females at each sampling period suggests that breeding is continuous, but no records are available for September through December. Young ranging from 31 to 46 mm were fairly common, and were estimated to be mostly in their second or third months. They were captured at the following times: 10 Jan.—31, 36, 38, 46; 18 Feb.—36; 1-2 March —32, 36; 16 April—37, 38, 42, 43, 45; 1 June—45; 16 Aug.—38. There are young of comparable sizes, and some smaller, from January, June, July and August (KU). The best population sample from my study area was obtained on 16-17 April 1968, and contained 20 individuals in a nearly continuous graduated series of the following lengths: 37, 38, 42, 43, 45, 51, 62, 65, 66, 69, 73, 76, 77, 77, 78, 82, 83, 84, 84, 92. Seemingly there had been no extensive gaps when reproduction was not occurring. It is tentatively concluded that in *A. lionotus* in the region of San Miguel, reproduction occurs throughout the year with no important seasonal change.

Anolis sericeus (Hallowell)

Description. Small, slender, with tail usually a little more than twice length, limbs medium (hind, adpressed, extends nearly to eye, and front to anterior part of muzzle); scales fine and heavily keeled, those of ventral surface larger; dorsal color ashy or with bronze suffusion and a silky sheen, with a series of about seven dark middorsal spots on neck and body, variably developed, continued onto tail as faint rings; sometimes a broad, pale middorsal stripe in female; undersurface dull, yellowish white with some dark stippling; faint dusky bars on limbs; dewlap large and well-developed in male, reddish-

orange with large central indigo spot (dewlap small in female with only a trace of bright colors); male somewhat larger and bulkier than female. (See Plate IV, lower.)

Range and habitat. Occurs from Tamaulipas southward to Isthmus of Tehuantepec, and through much of Central America at low and intermediate elevations, extending into Costa Rica on the west at least as far as Boca de Barranca. It is one of the most widely distributed of Central American anoles and occurs in a variety of habitats in forest, savanna, scrub, plantations and gardens. The localities where it was observed in my study represent the southern extremity of the geographic range. The preferred habitat is xerophytic, in woodland of open type or woodland edge or groves. The lizards were usually found climbing on tree-trunks or shrubs. At every locality where *A. sericeus* was found, *A. cupreus* was present in greater numbers, and it seemed that competition between them was reduced by vertical stratification, with *sericeus* generally at a higher level.

General habits. At each of the localities where it was observed, *A. sericeus* was found only occasionally. Uusually it was found on stems or tree trunks 0.3 to 2.6 m above ground level. Some ran to higher levels in escaping, and showed themselves to be skillful and rapid climbers. *A sericeus* is cryptically colored when on a background of tree bark, and like other arboreal anoles it has the habit of crouching flattened against a tree trunk or stem where it is easily overlooked.

Temperature relationships. Body temperatures (of Mexican and Guatemalan specimens that I collected in 1969 and 1970) were clustered in a six degree range, with a preferendum evidently between 32 and 33—notably higher than in most other species of anoles which have been tested (Fig. 16).

Reproductive cycle. Records are too few to show the trend of reproductive cycles but they do show seasonality of breeding. Eleven males and 10 females obtained in February of three different years at Playas del Coco, Sardinal, and Boca de Barranca were all adults (males 38-46 mm, females 35-46 mm). All the females were nongravid. A male taken in April and one in May were also adult. In August the only two individuals observed were a male of 25 mm on 17 Aug. (probably in its second or even third month and hence developed from conception in April or May) and a female gravid on 24 Aug. These few records indicate a breeding season beginning after the end of the dry season, probably in April, and lasting through the summer rainy season, but probably ending in August or September.

Anolis tropidolepis Boulenger

Description. Medium-sized, distinctive in having shortened head and, in adult male, conspicuously swollen tail-base; olive brown dorsally, dull white speckled with black ventrally, having a curved dark band between eyes and another on nape; male usually with series of middorsal black spots or pairs of spots, female often with pale middorsal band or a series of diamond-shaped middorsal marks (but almost unicolor in old individuals); male dewlap medium small, deep purplish red; females lack well defined dewlap, but have chin reddish even when immature; toes but little expanded distally; ventral scales keeled.

Range and habitat. A. tropidolepis is endemic to mountains of central and southern Costa Rica, the Cordillera Central and Cordillera de Talamanca, at altitudes of 1600 to 2600 m.

The habitat is cloud forest, and remnants of cloud forests where logs, snags, stumps, and occasional trees provide elevated situations and support dense growth

of epiphytes. The lizards are nearly always among epiphytes, in places where hollows and interstices provide abundant shelter, usually between ground level and a height of about 2 m. Occasionally they have been found in grass several meters from stumps or trees and have been found several times on eroded banks. In the wet climate of the cloud forest, grass and other low vegetation grow in a spongy mat providing effective shelter much like that of the epiphytes growing on tree trunks and stumps.

General habits. A. tropidolepis lives in a region of relatively low temperature and lacks the thermoregulatory behavior of most lizards. Body temperatures are therefore low and variable. Movements are relatively slow and clumsy compared with those of other lizards, but predators are scarce and hiding places are abundant and readily accessible. At any alarm the lizards disappear beneath screening vegetation and work their way downward through successive layers into cavities or crevices. Occasionally these anoles have been found on fence posts or bare surfaces of logs and stumps, but they do not regularly utilize look-out perches as do various other anole species. Because of the dense vegetation, this anole would usually be unaware of another nearby, and social interactions would occur only rarely, when two happened to meet. In confinement they display vigorously and fight when placed together.

Growth. There is much variation in rate of growth even between individuals of the same size, but growth averages slower than in other species. The rate usually exceeds 2 mm per month and sometimes exceeds 3 mm in young that are less than half grown. Young caught and marked when they appeared to be only a month or less old were recaptured as follows: 43 mm (minimum size of sexual maturity) at eight months, 43 mm at nine months, 46 mm at 11 months, 49 mm at 13 months. Attainment of full adult size, 52 mm, requires at least 15 months. Age-size correlation for an individual making typical growth is suggested in Table 3.

Spatial relationships. As shown in Figure 7, most of those recaptured, even after periods of many months, had moved less than 3 m. Such individuals were usually on the same tree trunk or stump. Movements up to 20 m, often involving a shift from one tree or stump to another, were fairly common. The longest movement recorded was 420 m (not shown).

Temperature relationships. Body temperature ranged from 12.4 to 26.5 in active *A. tropidolepis* (Fig. 10). There were few near these extremes, but the records were rather evenly distributed over the range 15 to 24 with no obvious preferendum. Laboratory tests showed that these anoles are able to feed at temperatures as low as 14 to 15. Air temperatures at times of capture ranged from 12.4 to 23.7, with the greatest concentration in the one degree range between 18 and 19, fairly typical daytime temperature on the study area. Body temperature usually approximated air temperature and was not consistently either higher or lower.

Reproductive cycle. In the area of my study, and probably throughout the species' range, uninterrupted egg production occurs (Fig. 9). Every adult female examined (143, from all months except July, October and December) appeared to be gravid and 21 that were dissected each had at least one oviducal egg. Uusually there were two oviducal eggs or an oviducal egg on one side and an enlarged follicle on the other. The size relationships of the eggs on the left and right sides varied greatly between individuals, implying that the time interval between ovipositions varies. From the records of marked females recaptured on successive occasions when they were unusually distended with eggs and appeared almost ready to lay, evidence was

obtained that an interval of approximately 30 days between ovipositions is typical. Each sampling of the study area demonstrated the presence of young of various sizes, including hatchlings, with no seasonality.

Basiliscus basiliscus (Linnaeus)

Description. Large, slender, long-legged (adpressed hind limb reaching beyond snout), long-tailed (2.0 to 2.6 times length), long-necked, with fine, granular dorsal scales, a short head, and 3 conspicuous dorsal crests arising as skin flaps from the head, body, and proximal part of the tail in the adult male; body crest extending from shoulder to pelvis, supported by 16 vertebral spines, caudal crest serrate, supported by 22 spines; in adult female only a rudiment of head crest is present with body and tail lacking crests; color is dull olive with a series of dark, transverse bands, one on neck and five on body, obscure in adults; a light line extending from below eye to shoulder; undersurface dull white; ventral scales of body smooth, subcaudals heavily keeled.

Range and habitat. Pacific slope of Nicaragua and Costa Rica through Panamá to western Venezuela, Colombia and northwestern Ecuador. It is chiefly tropical but occurs up to an elevation of 900 m; in Costa Rica it encroaches onto the Meseta Central almost to San José. It is partly aquatic and partly arboreal, is abundant along wooded streams, including some that are reduced to a trickle or to scattered pools in the dry season. In more humid climates it is less confined to the regular stream courses, being found on wooded hillsides and in open marshy areas. A typical habitat is a meandering woodland stream with undercut banks exposing root tangles; a dozen or more individuals will be found within a few square meters on logs and debris of a pile of drift, but intervening stretches of the stream may have few or none. Basking places like protruding boulders or logs beside or in the stream are an important requirement. (See Plate II, lower.)

General habits. A young one approached by a person in its usual surroundings at the edge of the water runs across the surface to the other side. Dashes of usually less than a meter are typical when the lizard is in the vicinity of adequate cover, but those flushed in relatively open situations may run farther, moving over the surface of the water with a brisk bipedal trotting gait, either upstream or downstream, without being deterred by swift water or riffles. However, the relatively bulky adults are much less adept than the smaller lizards at running on water. An adult dashing out into a stream rapidly loses its momentum and sinks; then it submerges and swims away underwater. The young swim and dive well, but have a greater tendency to remain on the surface. The dash of a flushed individual is always toward shelter. These basilisks are remarkably shy; a slight movement of a person 30 m or more from the stream may send several scampering toward shelter. Unless the alarm is severe, the lizard usually stops short of actual concealment, pausing at the edge of the thicket or pile of drift to watch.

Individuals vary in shyness, but usually adults are much shyer than young. Adults tend to stay in the immediate vicinity of shelter and at an alarm usually duck into concealment and remain hidden for a lengthy period, then emerge slowly and cautiously. Young are often found in the open and one sometimes can be approached time after time and it only moves away without concealing itself.

These basilisks climb trees both to escape and to forage. One that is flushed while on or near a tree trunk may climb even though abundant hiding places are available at ground level. Movements of a

person below may cause a lizard to climb higher by several stages until it is on the outermost twigs. Then, if sufficiently alarmed, it may plunge into the stream below. A person following the edge of a stream or wading in it may cause individuals in trees along the bank to plunge into the water. Larger ones submerge immediately, but small ones strike the surface with so little force that they do not submerge, and skitter away on the surface. The climbing habit is less common in young than in adults.

Growth. For 10 recaptured, gains in length were 44 to 52 in 35 days, 45 to 57 in 46, 49 to 69 in 52, 49 to 95 in 196, 74 to 81 in 39, 81 to 86 in 39, 86 to 91 in 16, 110 to 133 in 86, 53 to 108 in 331, and 88 to 134 in 322. The last two in this series were females and the preceding two were males; in the others sex was undetermined. The trend of the records suggests that sexual maturity is attained at an age of one year or a little less (while the lizards are still far short of adult size). Males continue to grow longer and attain a much larger size than females. Tentative age-size correlation is shown in Table 3.

Spatial relationships. Only 13 definite records of movements in the marked basilisks were obtained, and distances ranged from 0 to 56 m for intervals that averaged 48 days. However, one female marked as a juvenile and recaptured after 293 days had moved an estimated 116 m.

Immatures that are flushed in the open may make dashes of 25 to 30 m, so their home ranges must be at least this large in diameter. However, each large individual has a refuge toward which it runs when alarmed. Also, adults are more exacting in their requirements, staying much closer to shelter and possibly having smaller home ranges than juveniles.

Temperature relationships. Seventeen body temperatures were obtained, all in the range 25 to 34. Figure 17 contrasts these with body temperatures of *Ameiva undulata* at the same localities. The *B. basiliscus* temperatures averaged several degrees lower with little overlapping. The basilisk temperatures were all from active individuals, caught in the daytime, and not including those known to have been in the water recently.

Reproductive cycle. Ortleb (1965) reported a female found laying 18 eggs at Barro Colorado, Panama Canal Zone, on 24 July, and these eggs hatched after 77 days incubation. Corpora lutea (9 Feb.), uterine eggs (8 and 10 Feb.) and enlarged follicles (24 Aug.) in females from Finca Taboga and La Irma indicated clutches of 9, 6, 4 and 6. Lengths of females were 152, 148, 146 and 133.

The available records clearly indicate seasonal trends. Usually the lizards were seen too fleetingly or at too great a distance to judge their reproductive states. One female seen at La Irma 11 Feb. 1970 ap-

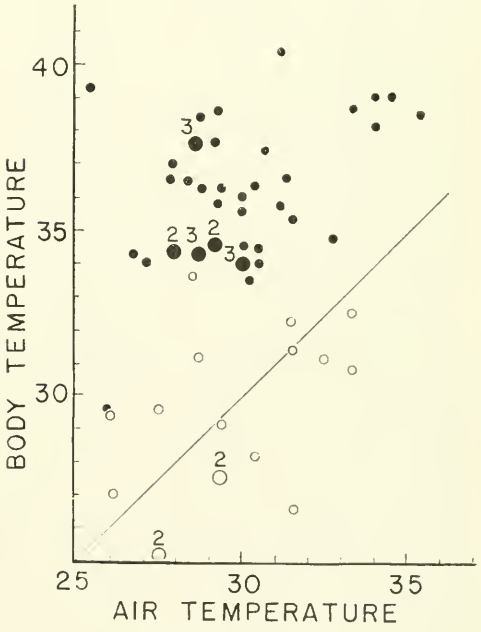

Fig. 17. Body temperatures and adjacent air temperatures of *Ameiva undulata* (solid circles) from La Irma and Sardinal and of *Basiliscus basiliscus* (open circles) from La Irma. Small and large circles show numbers as in Figure 10.

peared gravid, as did another seen there on 16 May 1968 and several seen at Finca Taboga on 18 May and 6 July 1968. However, only nongravid females were recorded at La Irma 1 Feb. 1970 (1 dissected), 9 Feb. 1969 (1 dissected), 19 Feb. 1968 (2 dissected), 23-24 March 1968 (5 dissected), and 1 April 1968 (at least 1 seen). Others were recorded at Finca Taboga 17 Feb. 1970 (1 dissected), 18 March 1965 (11 dissected), 26 March 1968 (at least 11 seen). At Río Naranjo near Boca de Barranca, 10 March 1970, 11 females dissected were all nongravid but had enlarged oviducts indicating recent egg-laying. At an upland locality, Turrúcares (27 km W San José), on 9 March 1970, 2 females dissected were nongravid. These records indicate that most females are not carrying eggs during the dry season.

On every occasion when populations were sampled, young constituted a high proportion of those seen. Uusually they were especially concentrated in one or two size groups, providing a basis for estimating the times when most hatching occurred. Table 4, extrapolating to times of concentrated egg-laying on the basis of dominant size groups of young in 11 large samples from 5 localities, indicates that laying occurs from July to February but is much reduced during the remainder of the year (Fig. 18).

The streambank habitat is subject to drastic alteration when the streams overflow and cut new channels. At such times the eggs may be destroyed in such large numbers that the population structure is altered subsequently, lacking certain age groups of young. In each large sample young of various sizes were present, but certain size classes were especially well represented.

Basiliscus plumifrons (Cope)

Description. Large, slender, fine-scaled; bright green; eye red; conspicuous middorsal crests on head, body, and tail in adult male; head crest double with small anterior part arising behind level of eye, connected at its base with much longer and larger occipital part, body crest arising behind forelegs, low anteriorly but prominent posteriorly, ending just anterior to thighs, supported by dorsal spines of 17 thoracic and lumbar vertebrae, caudal crest confined to basal third of tail, supported by vertebral spines, body and caudal crests with scalloped edges, head crests rounded; limbs and toes long and slender; tail often 2.5 or more times length.

Range and habitat. Caribbean slope of Costa Rica at low and medium elevations, north into Nicaragua and south into Panamá. This basilisk is usually associated with water; both aquatic and arboreal tendencies are marked. At Portéte it was ob-

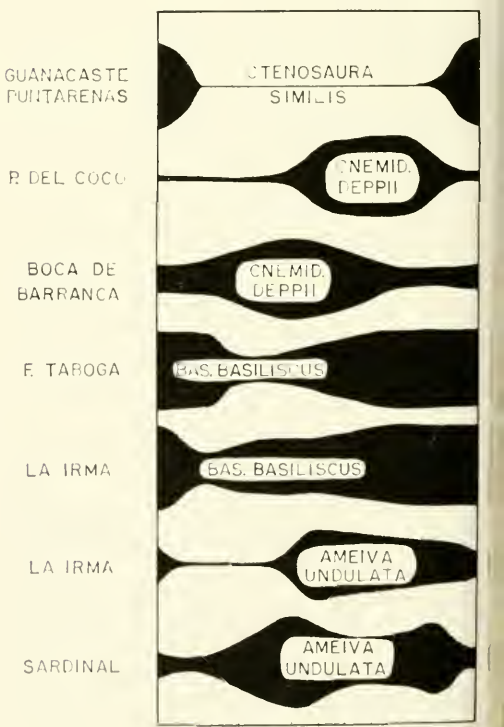

FIG. 18. Relative levels of egg production through the year in 7 lizard populations of the Pacific versant in areas having a severe dry season.

served in coconut groves, among coral rock and logs at the beach, and along an overgrown concrete wall; at Beverly it was observed in swamp, in cacao, along streams in forest remnant and forest edge. At San Miguel de Sarapiquí and Cartago it was found among boulders at the edge of a swift mountain stream. Hirth (1963a), in his study at Tortuguero, found *B. plumifrons* associated with the more common *B. vittatus*. In commenting on their habitat differences, he stated: ". . . *B. plumifrons* is fairly abundant in trees along the riverbank. It is more arboreal than *B. vittatus* and also is more likely to be found in shaded situations."

General habits. *B. plumifrons* is essentially similar to *B. vittatus* in habits, except as noted above.

Growth. Of several young caught and marked at Portéte, only one was recaptured. At the original capture on 4 Sept. 1968, it had a length of 91 mm. On 30 Jan. 1969 it was recaptured at the same spot and had grown to 113 mm. Presumably growth rate parallels that of *B. vittatus* except that at any given age individuals of *plumifrons* average a little larger and grow a little faster. If so, the one recaptured probably was about seven months old when first recorded.

Basiliscus vittatus Wiegmann

Description. Large, slender, long-legged, long-tailed, with relatively long neck, short head, and fine granular scales; male with conspicuous triangular, middorsal crest, based from behind the eyes to mid-neck, and directed backward; a low inconspicuous crest of enlarged, raised scales along middle of back and extending onto the tail, which is somewhat compressed; in female head crest is represented by a much smaller flap of skin rounded posteriorly, not pointed as in the male; on legs scales are larger than on body, and heavily keeled; ventrals keeled; ground color olive brown, with pale middorsal stripe and a pair of pale narrow dorsolateral stripes arising behind eyes and fading on rear of body; a series of obscure, dark transverse bands on body and tail; undersurface dull white.

Range and habitat. *B. vittatus* occurs in tropical lowlands from Tamaulipas and Jalisco in México through Central America to Colombia and Ecuador. It is present on both coasts of Central America but

Table 4. Time of breeding of *Basiliscus basiliscus* indicated by dominant age classes of young at various time and places in Puntarenas and Guanacaste provinces.

Time of sample	Place of sample	Length of dominant class of young	Estimated age of young (months)	Hatching time indicated	Laying time indicated
late Nov. 1967	F. Taboga	60-70	1-2	Oct.	July-Aug.
late Feb. 1970	Ojo de Agua (850 m, 16 km W San José)	about 80	3	Nov.	Sept.
late March 1968	La Irma	70-89	2-4	Nov.-Jan.	Sept.-Nov.
early Feb. 1970	La Irma	about 60	1	early Jan.	Oct.-Nov.
early Feb. 1970	Río Naranjo (6 km N B. de Barranca)	40-50	0.5	late Jan.	early Nov.
late Feb. 1970	Ojo de Agua	40-50	0.5	Feb.	early Dec.
late March 1968	La Irma	43-63	1	late Feb.	Dec.
Feb.-March 1970	Turrúcares (639 m, 27 km W San José)	40-50	0.5	mid-Feb.	early Dec.
early April 1968	Río Naranjo	about 60	1	early March	Dec.
mid-May 1968	La Irma	44-53	0.5	April-May	Feb.
mid-May 1968	F. Taboga	40-50	0.5	May	Feb.

seems to be absent from extensive areas of the Pacific lowlands in Costa Rica, where there is a pronounced dry season.

It is mainly terrestrial but has aquatic and arboreal tendencies. It lives in rain forest and forest edge, along streams, in swamps, in gardens and plantations. A favorite habitat along the coast is in coconut groves, and the large piles of rotting coconut husks provide the perches and escape shelter that the lizards require. In the groves or adjacent to them jagged coral blocks, logs, beach wrack, tangles of shrubs and vines, and mats of low vegetation also are used for shelter.

General habits. Several authors have described the habits of this species, especially Hirth (1963a) who studied it at Tortuguero in Costa Rica 79 km northwest along the coast from the localities of my study, but in similar beach habitat. Banded basilisks are strictly diurnal and heliothermic. For the night they may climb to perches such as the mid-rib of palm fronds, average 1.4 m above ground (Hirth 1963a), and sleep in the open. Probably some sleep concealed beneath objects also; individuals basking on piles of coconut husks in late afternoon were often observed to retreat into the pile as the temperature dropped and shade fell over them, and they did not reappear.

The lizards are wary, but escape behavior varies greatly according to the situation, the temperature and size of the individual. Flushing distance, as a person approaches, varies from one to 30 m, at least. Typically the aroused lizard makes a dash sometimes as long as 30 m but usually much shorter, taking it away from the approaching person and to or near shelter. If followed, it is inclined to flush again without allowing such close approach as it did at first, and to retreat to a more sheltered situation. An adult that is flushed often ducks out of sight into a hole or other refuge whereas a juvenile sometimes can be approached time after time, and merely retreats without effectively concealing itself. An estimated 10% of the lizards that were flushed ran to trees, usually coconut palms, and climbed beyond reach. More often the lizards ran to or across water in escaping.

Part of the study area, inland from the front dune, was low and swampy and often inundated after heavy rains, with water standing to a depth of 0.1 m. After relatively rainless periods the area lacked standing water but soil was still damp, and the lizards were attracted to such low wet areas.

Hirth (1963a) examined the contents of 320 stomachs from Tortuguero and found a variety of arthropod prey, with tenebrionid beetles, ants, grasshoppers, amphipods, lycosid spiders and lepidopteran larvae especially well represented. In the young the food consisted of animal matter exclusively, but in adults plant food was common, including grasses, seeds, stems and berries. In six adults the stomach contents consisted entirely of plant material.

Since the male is much larger, with highly developed display organs, and since adults tend to stay in certain small areas, it is plausible to assume that these lizards are territorial. However, territorial behavior was not observed either in the course of my field work or in Hirth's study.

Growth. At Portéte 35 recaptures were made after substantial intervals, showing growth. For the 13 considered most representative, gains in length were 46 to 59 to 76 to 86 in 52, 92 and 81 days; 50 to 65 in 51; 54 to 64 in 52; 57 to 64 in 31; 59 to 76 in 92; 64 to 69 in 31; 51 to 78 to 105 in 139 and 232; 53 to 120 in 78; 76 to 84 in 34; 79 to 86 in 51; 49 to 121 in 125; 61 to 113 in 332; and 79 to 98 in 142. The first six of these individuals were of undetermined sex and the last two were females; others were males.

Hirth (1963a) obtained more records for the early stages of growth. For 11 hatchlings (35-40 mm) he found a mean growth rate of 7.5 mm in 15 days and for 16 in the length range 41-50 he recorded a mean of 6.3 mm for the same period. Thus for the first month of life length gain of about 15 mm to a little more than 50 mm may be considered typical. For those of 51-60 mm length he found an average gain of 5.1 mm in males, 5.0 mm in females per 15 days, and in the 61-70 mm group, corresponding figures were 3.9 (♂) and 2.9 (♀) mm. His data were meager for lizards between 70 and 100 mm but my own data are more adequate for this range. The tentative age-size correlation shown in Table 3 is suggested as most typical for males. For females the growth rate is somewhat depressed, especially in the middle and late stages of growth.

In my study the smallest gravid female was 87 mm. Hirth (1963a) recorded one of 83 mm having oviducal eggs, and he recorded males to be sexually mature at a minimum size of 80 mm, but only five of 18 that were 80-89 mm contained spermatozoa. Seemingly sexual maturity ordinarily is attained at an age of about 6 months, but the lizards continue to grow until they are at least twice that age.

One female marked as an adult of 108 mm on 23 Jan. 1968 was recaptured on 12 June 1968, 3 March 1969 and 4 March 1970. Her length had increased to 109 at the second capture and 111 and 118 at the third and fourth respectively. She must have been at least one year old at the time of her first capture and hence was more than three years old at her last capture. A male marked while probably still in his first month of life had records spanning 28 months and at his last capture he was of adult size but not especially large. The fact that two of these 24 basilisks recaptured spanned more than two years with their records indicates that their longevity is relatively great compared with most small lizards in the tropics.

Spatial relationships. Hirth (1963a) found that *B. vittatus* of all ages and both sexes regularly occupy small home ranges from a minimum of 7.9 m^2 to a maximum of 19.8 m^2. The home ranges in his study were polygons plotted on the basis of 13 to 16 recaptures. Ranges were found to average a little smaller for males than for females, and a little smaller for adults than for young. "Mature basilisks . . . have a strong attachment for a certain region within their home range. This is usually a pile of coconuts, which serves as both a basking and a feeding site."

In my study, 29 movements were recorded after an interval of a month or more. The longest distance was 152 m, and shifts of 79, 62, 43, 43, 41, 37, and 37 m were also recorded, but most movements were in the range 4.6 m to 23 m. These records suggest considerably more mobility than found by Hirth, and probably reflect alterations or shifts of home range over periods of months, as available cover and other habitat features are altered by flood and drought, tide, or human activity.

Temperature relationships. Hirth (1963a) obtained body temperatures of 476 juveniles and 242 adults. In both groups 35 was the preferendum, with progressively fewer records for each half-degree up to a maximum of 38.5 (with just one record). The lowest body temperature was 23.5. Substrate temperature was most often about 32.5 and air temperature about 29.5. Hence, usually a body temperature was several degrees warmer than either the air or the substrate, emphasizing the heliothermic tendencies of this basilisk. Hirth indicated the following thermal thresholds for *B. vittatus:* minimum voluntary tolerance 23.5 to 26.5; basking range 26.1 to 33.0; normal activity range 33.1 to 37.5; ecological optimum 35.3

(±.05) for juveniles and 34.7 (±.07) for adults; maximum voluntary tolerance 36.6 to 38.5; critical maximum 41.0 to 44.6; lethal 41.0 to 47.0.

Reproductive cycle. At Portéte there were obviously gravid females in the series captured in October 1967 and March, May, June, August and September 1968 but several captured in January 1968 and 1969 did not appear gravid. In both January samples there were hatchlings (from eggs laid in October?) and larger numbers of older young as well as adults. In March samples there were no hatchlings. The 15-16 March 1968 and 4-6 March 1970 samples contained second- and third-month young, but the 1-3 March 1969 sample contained only those in their 3rd month (minimum 63 mm) and larger. In all three March samples there were many young in the 70-85 mm size range, three to five months old, hatched October to December from eggs that were laid mostly in August and September. A sample from 6-9 May 1968 had a group of hatchlings (presumably from eggs laid in late February) and many large young 68-101 mm, about three months old or older, but no young of intermediate sizes. A three-month pause in breeding extending over part of November through January and part of February is indicated. A sample for 11-14 June parallels the early May sample, except that both the principal groups of young have made further growth. The hatchling group has not only newly emerged young but others of various sizes up to 55 mm, perhaps five or six weeks old. The previous crop of young, now at least four months old have minimum lengths of 76. Samples from 29-31 Aug. 1969 and 2-4 Sept. 1968 have hatchlings and older young of graded sizes, indicating continuous reproduction throughout the spring and summer months. The 28-30 Oct. 1967 sample is notable in having a high proportion of young, representing all sizes from hatchlings up to adolescents, and indicating a high level of reproductive activity continuous for many months previously.

In summary, the combined evidence, from reproductive state of adult females and from occurrence of young of various sizes, indicates a breeding season beginning in mid-February or a little earlier and continuing through October. In November egg-laying is greatly reduced and it remains at a low level through December and January (Fig. 8).

An adult female captured and marked on 6 May 1968 was judged to be gravid but was not much distended. Probably she had ovarian follicles that were still not mature and these may have been destined for her second clutch, as there is much egg-laying in February and March. The same female was shot on 4 Sept. and then contained uterine eggs nearly ready for laying. An output of four clutches per breeding season seems a reasonable estimate but on the conservative side.

The data concerning growth indicate that females mature in time to conceive approximately a year from the time of their own conception. Those conceived toward the end of one breeding season might contribute one small clutch of eggs at the end of the next breeding season, or they might postpone reproduction until the third breeding season. For example, a female of 46 mm was caught and marked on 23 Jan. 1968, when probably still in her first month of life, and was recaptured on 16 March, 14 June and 4 Sept. 1968. She made typical growth, and on 4 Sept. had attained the minimum size of sexual maturity (86 mm) and had enlarging ovarian follicles (2.5 mm) that might have matured by the end of October.

At Tortuguero, Hirth (1963a) found juveniles to be present during every month of his study—June through September and January through April—but they were most numerous in August and September.

Probably the Tortuguero population conforms with the seasonal trend that I found at Portéte, but Hirth was not on hand to observe the October to December build-up to the maximum numbers of juveniles and he did not specifically mention the scarcity or absence of hatchlings in March and April.

In 12 instances the number of unlaid eggs was determined in Portéte females by palpation of captured animals that were almost ready to lay, or by dissection, and in every instance there were 2, 3 or 4 eggs, $\bar{x}=3.17\pm.20$. In nine females from southern México (KU) clutches were larger, with from 3 to 5 eggs, $\bar{x}=4.10$. Hirth (1963a) found an average of 4.2 eggs in 25 females at Tortuguero. I found clutches of 3, 5 and 6 eggs in females at Barro Colorado in the northeastern corner of Costa Rica. For the 49 clutches combined the average is 3.90, range 2 to 6.

Ctenosaura similis (Gray)

Description. Large, stocky, body flattened with stout, moderately long limbs and tail (more than twice length in hatchlings but less than twice in adults), scalation on body fine and granular, on tail in whorls that are relatively coarse and spiny; a crest of erect, spinelike middorsal scales on body; a gular pouch and transverse gular fold; color dull black with pale tan patches in adults, bright green with dark markings in small juveniles, tan with dark reticulations in hatchlings.

Range and habitat. This ctenosaur occurs from the Isthmus of Tehuantepec on both coasts in southern México south to Panamá on the Pacific versant. It is abundant chiefly in low, hot areas having a pronounced dry season. In Costa Rica it extends onto the Meseta Central nearly to Alajuela, 900 m.

The preferred habitat is open woodland or savanna. Hollows in limbs, tree trunks or fence posts, or burrows beneath tree roots, old buildings or rock piles provide shelter.

General habits. C. similis is both terrestrial and arboreal, largely herbivorous but also predatory. The hatchlings are strikingly different from adults in behavior as well as appearance. At first strictly terrestrial, they are much more slender and agile than the adults and are alert and active; small insects are their main food (Montanucci, 1968). There is gradual transition to the relatively bulky, phlegmatic, partly arboreal, largely herbivorous adult. The adult browses rather indiscriminately on tender herbaceous vegetation, but also preys on various small vertebrates and large insects.

A hatchling, when followed, will run from one clump of vegetation to another, increasing the length and speed of its dashes if it is hard pressed, but not relying on any regular refuge for escape. While still less than a month old, it becomes somewhat scansorial, perching on tree trunks, fence posts, or boulders, climbing to escape in times of danger and returning to regular retreats for periods of inactivity.

The adults are strongly attached to their retreats and use elevated perches nearby, ducking into shelter at any disturbance. Adults are much shyer than young. At times they will scurry for shelter when a person is as much as 65 m away, especially when surprised in an open situation such as a beach or cultivated field. However, one that is near shelter may allow a person to pass within a few meters without moving. At Finca Taboga many inhabited hollow fence posts and would habitually bask on top of the posts, ready to scuttle into the cavity at any alarm. Elsewhere, hollow trees, logs or boulders provide basking places that have secure shelters within or beneath them. Often the retreat is a burrow in the ground probably excavated or enlarged by the lizard. Taylor (1956:182) stated: "Often a

large tree, especially if there is a hollow trunk or hollow limbs, offers shelter to a colony of ten or more of these large lizards. From here they may forage a hundred yards or more in varying directions." Doubtless this species is territorial as is *C. pectinata* studied by Evans (1951), but where several or many live crowded in close proximity there are likely dominant and subordinate individuals. Judging from the homeward dashes of flushed individuals, forays of "a hundred yards" are possible but are relatively rare, and the usual foraging radius is much shorter. The recapture records of first-year young indicate that these lizards are confined to remarkably small home ranges.

Growth. For 8 recaptured, gains in length were 65 to 74 in 36 days, 72 to 84 in 33, 70 to 78 in 33, 70 to 78 in 31, 73 to 84 in 31, 76 to 99 in 45, 86 to 143 in 228, and 95 to 170 in 162. All these growth periods were in the rainy season. The last two records listed are especially significant because they span relatively long intervals. The last one listed grew at almost twice the rate of the one just before it. Thus a wide range of individual variation in growth is indicated. Table 5 shows the trend of growth into the third year based on recognizable size groups of young; measurements or estimates of length were made on substantial series. Age-size correlation for an individual making typical growth is suggested in Table 3.

By the time the young are a year old they have more than tripled in length, and are approximately half the length of adults. By the following winter they have become sexually mature but are still much smaller than average adult size. The clutch is large and variable with great increase from first to second clutches and especially to those of large adults. The fact that hatching extends over several weeks in any one locality suggests the possibility that a female may produce a second clutch. Because of the high productivity, young sometimes appear in great abundance in places where the adults are not especially in evidence.

Spatial relationships. In 16 instances I recorded distances between captures for first-year young recaptured several weeks after they were originally marked. The 4 longest movements were respectively 131, 55, 49 and 46 m; the remaining 12 were all in the range 4 to 16 m and averaged 10.4.

Temperature relationships. Ctenosaurs are limited to warm climates and are heliothermic. The 54 body temperatures obtained, all from juveniles (Fig. 12), indicate a preferendum between 36 and 37. Ctenosaurs were caught most often at air temperatures between 29 and 31, and their body temperatures were from four to eight degrees above air temperatures. Doubtless temperature relationships are similar in adult ctenosaurs, except that their relatively bulky bodies change more slowly than those of the young in response to environmental change. Ctenosaurs spend much of their time basking in sunshine, even when temperature is relatively high. Absorption of heat may be reduced by position and orientation; for instance, one perched on a fence post may have only its head exposed to sunshine, absorbing relatively little heat in the warmer part of the day.

Reproductive cycle. C. similis proved to have the most restricted breeding season of any of the lizard species studied (Fig. 18). Hatching is limited to a period of weeks from late April to June. Incubation is mainly within the dry season. At Boca de Barranca on 9 Feb. 1970 a female of 212 mm was found to contain 21 oviducal eggs 24 x 18 mm and probably almost ready to be laid. This female was of a size typical for ctenosaurs late in their second year. At El Salto, Escuintla Province, Guatemala, a female of 262 mm on 17 Feb. 1971 contained 34 oviducal eggs each about

30 x 19 mm. Adult females dissected at Finca Taboga 18 March 1965 (2), Playas del Coco March 1965 (1) and Finca Pacifica (15 km NNE Finca Taboga) 25 May 1968 (1) all had enlarged oviducts but minute ova and obviously had completed their egg-laying for the season.

Alvarez del Toro (1960:93) stated the incubation period to be 90 days. Perhaps it is somewhat less in many instances. Most egg-laying must occur in December and January with some in November and February. At Tilarán, 562 m, 30 km NE Finca Taboga, in a cooler and wetter climate than that usually inhabited, young estimated to be 120, 110 and 110 mm were seen on 25 December 1967. They were smaller than any of the numerous young seen at low altitudes in the same week and seemed to be retarded by at least two months compared with these young. Presumably the cumulative effects of decreased insolation and lower temperature delayed the breeding season, extended incubation, and slowed the growth of the hatchlings to bring about the differences observed. At Quepos, also, in December 1967 and January 1968, young were observed to be relatively small as compared with those in Guanacaste, and nearly as much retarded as those at Tilarán. However, newly emerged hatchlings were found at Quepos on 1 May 1968, somewhat earlier than they appeared in Guanacaste. Retardation of young at Quepos presumably was the result of persistent overcast and relatively low insolation during the summer and autumn months of high precipitation, re-

Table 5. Lengths* of young *Ctenosaura similis* showing the trend of growth.

	Guanacaste highways no. 1 and 21	Playas del Coco and Sardinal	Finca Taboga† and Boca de Barranca	Quepos
First year				
early March				60 (in one)
early May				69 (65-78 in 5)**
late May		59.4 (56-63 in 24)**	70.7 (57-82 in 48)†**	
late June				77.4 (60-90 in 21)
early July		71.2 (63-97 in 24)**	83.8 (63-107 in 52)†**	
mid-Aug.	91.5 (77-110 in 42)			
late Aug.				85.0 (70-105 in 20)
late Nov.			135 (110-175 in 25)	
late Dec.	151 (120-190 in 28)		129.5 (120-140 in 10)†	
Feb.	165 (150-180 in 6)	143 (115-180 in 15)**	149 (120-170 in 10)	
Second year				
April			162 (130-190 in 40)	
May	168 (140-190 in 6)**		162.3 (110-200 in 26)	138 (125-150 in 3)
July	166 (130-190 in 16)	196 (177-220 in 4)**		
Aug.	171.5 (143-216 in 34)			163 (160-170 in 3)
Nov.			211 (190-220 in 16)	
Dec.	217 (200-250 in 19)			
Feb.	211 (190-240 in 8)		205 (180-240 in 13)	
Third year				
April			222 (190-280 in 30)	
May	225 (200-260 in 8)		230 (210-290 in 18)	
July	245 (200-290 in 12)			

* Means, extremes and numbers in samples.

** Measured (other records are estimates).

† Finca Taboga; other series in column 4 represent Boca de Barranca.

ducing the time available for feeding and other activities.

Iguana iguana (Linnaeus)

Description. Giant iguanid, having a middorsal crest from nape onto tail, consisting of a series of greatly enlarged, sickle-shaped scales; crest longest at middle of neck, tapering abruptly anteriorly but very gradually posteriorly on body and tail; head short, with large, prominent eye, with a large circular scale at angle of jaw which exceeds both ear and eye in diameter; a pendulous nonextensible dewlap (more prominent in male) bordered posteriorly by a transverse fold, and having a midventral series of much enlarged, flattened, denticulate scales anteriorly; tail somewhat compressed, attenuate and whiplike, 2 to 2.5 times length; scales fine and granular, tending to form regular transverse and longitudinal rows on body, limbs and tail; color predominantly green, but with series of several sometimes obscure, wavy black transverse bands on body and tail; in old males ochraceous or orange suffusion tends to replace green of dorsal surface.

Range and habitat. Humid tropical lowlands from Sinaloa and Veracruz through southern México, Central America and into South America. The habitat is in forest and forest edge, especially along streams.

General habits. Iguanas climb rapidly and easily; in tall trees they appear to be secure and at ease even in the presence of humans or natural enemies. These herbivores find much of their food in trees and take tender foliage, flowers and fruits of many kinds, but the diet includes some animal food, especially in young. Iguanas have an affinity for water, and this is especially noticeable where the species occurs in a relatively dry climate. There the population is concentrated along streams and rivers. The lizards enter the water readily, and swim well. Usually they submerge while swimming, and with leisurely movements of the long flattened tail, progress rather rapidly through the water. Much time is spent in trees over the water. Characteristic behavior of one that is approached while in a tree too small to provide security is to plunge into the stream and swim beneath the surface to a protected spot beneath an overhanging bank, behind exposed tree roots, or in dense vegetation. Iguanas may swim far from shore, in rivers or even in the ocean. They have some gregarious tendencies; many of both sexes and various sizes may congregate in a single tree where there is an attractive food supply, and many females may gather in a small area for egg-laying (Rand, 1968).

Reproductive cycle. Although the iguana occurs mainly in warm moist climates that have relatively little seasonal change, there seems to be a well defined annual breeding season, most females laying their eggs within a period of weeks, and young appearing in large numbers at about the same time each year. In Chiapas, southern México, breeding occurs from October to December and eggs are laid in March or April according to Alvarez del Toro (1960:89). However, Neill and Allen (1959) found hatchlings in April in British Honduras. At Tortuguero in northeastern Costa Rica, Hirth (1963b) found that egg-laying occurs in the March-April dry season, and hatching coincides with the arrival of the summer rainy season. Hatchlings have been found emerging on 6 June. At Barro Colorado in the Panama Canal Zone, Rand (1968) found a relatively advanced breeding schedule. From the end of January to the first week of March an estimated 150 to 200 gravid females swam across a narrow channel and deposited their eggs on an open area of an islet. Hatching was concentrated in the last weeks of April or the first week of May,

coinciding with the onset of the rainy season.

The following observations made in the course of my study, in western Costa Rica, indicate concentration of egg-laying there in January and February.

28 Dec. 1967, Sardinal: Female of 410 mm contained 17 follicles 28 mm in diameter.

17-18 Jan. 1968, Quepos: Egg-laying seemingly at a peak; groups of people hunting iguanas with dogs and carrying gravid females captured when they came to the ground to deposit their eggs.

11 Feb. 1970, La Irma: Females noted excavating nest burrows at several places along streambank; group of 4 flushed from their unfinished burrows within space of 9 m.

15 Feb. 1970, Playas del Coco: Female distended with eggs flushed from gully.

17 Feb. 1970, Finca Taboga: Nesting in progress with many open burrows in sandbanks; as many as 4 females flushed simultaneously from burrow areas.

The presence of young of different sizes in a single sample suggests an extended breeding season, but variation in hatchling size and different growth rates complicate reconstruction of the breeding cycle. The sizes of 8 juveniles from my study areas at Playas del Coco and Boca de Barranca suggest hatching as early as mid-December or as late as early May. Twenty-two juveniles (KU) from scattered localities in Costa Rica and southwestern Nicaragua had a mean length of 78±1.17 (70-87). Presumably their average age was a little more than a month, and their hatching must have been concentrated in early May from eggs laid in late February or early March.

The protracted period of egg-laying raises the possibility of multiple clutches, but is is not known whether a female occasionally or regularly produces more than one clutch in a season. Another unsolved problem is the time required to attain sexual maturity. At Finca Taboga in April 1968, when many iguanas could be observed simultaneously climbing in the same large tree, there were at least three size groups distinguishable: 1) adults more than 300 mm (usually more than 400) in length, 2) young about half the length of the adults, 160-170 mm, and 3) young about one-fourth the length of the adults, 75-90 mm. Possibly some iguanas breed when they are two years old, but it would not be surprising if normally more than two years were required to reach maturity.

Sceloporus malachiticus Cope

Description. Medium-sized, coarse-scaled, with scales heavily keeled and spine-tipped; tail about equal to length in young, a little longer in adults; color greenish tan with nine or ten pairs of dark dorsal spots in juvenile and adult female, yellow-green with no well defined dorsal pattern in male; ventral surface with paired longitudinal deep blue areas separated by black medially; female and young have smaller and paler blue areas and lack the medial black.

Range and habitat. S. malachiticus occurs from Honduras and El Salvador into Panamá. In Costa Rica it is absent from low elevations, but occurs over a wide altitudinal range from about 650 m up to more than 3000 m.

Its habitat is in relatively open, sunny situations, such as woodland edge and clearings, fence lines having live trees (some with cavities), and logs, woodpiles, gardens, rough-barked trees, rock walls, tile roofs of buildings, pasture and meadowland where there are occasional boulders or outcrops and thorny bushes for shelter. The species occurs over a wide

range of climatic conditions, from high montane cloud forests to xeric forests of scrubby and thorny type.

General habits. Like other members of its genus *S. malachiticus* is a heliotherm; the basking habit is especially noticeable where the species occurs in relatively cool climates. A characteristic location for basking is the top of a boulder or fence post. In such situations the lizards are conspicuous and may be seen from a distance. As the day becomes warmer, they leave their basking spots and move to the shaded side of the post or boulder, usually with head directed downward, prepared to make a rush to the ground to catch any prey that passes. The lizards are shy, may take alarm at a person 15 m or more away, and cannot be easily stalked. One that is approached moves toward shelter and if further disturbed it will scramble into a secure place of concealment, beneath a boulder, into a rock crevice, or into a decaying stump or log, or in a cavity of a limb. The dash to shelter is usually only a few meters at most, indicating that home ranges are small, but over a period of weeks a lizard may shift from one tree or rock outcrop to another, abandoning temporarily at least the site of its earlier activities. Young are more terrestrial than adults, are less shy, and less adept at escaping and finding adequate shelter. A juvenile that is flushed may run from a boulder and seek concealment in a tuft of grass or beneath a pebble where it can be easily caught.

Food consists of insects and arachnids. A litter of young born in confinement ate termites avidly but was relatively indifferent to other small insects of similar size. As in other species of *Sceloporus*, ants probably figure prominently in the diet.

Growth. Because the extreme wariness of the lizards intensified with stalking and capture, recaptures of marked individuals were few. For 2 recaptured males gains in length were 36 to 38 in 14 days and 44 to 56 in 53. For 7 recaptured females gains in length were 33 to 64 in 167 days, 35 to 36 in 14, 40 to 43 in 14, 40 to 44 in 19, 46 to 48 in 14, 44 to 48 in 92, and 48 to 64 in 105. Except for the last one listed, all these growth periods were mostly or entirely within the dry season. For the entire group growth averaged 4.6 mm per month, but with much difference between individuals. A sample of five young on 10 Dec. 1967, soon after birth, averaged 31.7 mm, and 139 days later on 28 April, another sample of 11 presumably born at the same time averaged 53.6 mm. Thus here normal growth averaged at least 5 mm per month for several months. Sexual maturity is attained by females still far short of average adult size, and growth continues through and beyond the first year of life. A female measured (48mm) and marked on 28 April and recaptured on 11 Aug. appeared to be gravid on the latter date and was approximately the minimum size (64 mm) of sexual maturity. Age-size correlation is suggested in Table 3.

Spatial relationships. Of 8 recaptured lizards, 2 (both young females) were recovered at the original location after 13 days and 19 days. Others had moved distances of 1.2, 1.5, 3.0, 4.6, 9.1 and 21 m in intervals of 14 to 105 days.

A typical home range seems to encompass only a few square meters and is located with reference to a secure shelter, with an adjacent elevated perch for basking. The home range, or at least its central area, is defended as a territory. An adult male and female are often found in close association, but members of the same sex are well spaced. As a result of this spacing, territorial encounters between adults have not been observed but young of various sizes have been seen to display toward others and chase them.

Temperature relationships. Eighty body temperatures were obtained. Two lizards

that were inactive (beneath a log and in a hollow stump) had temperatures of 15.7 and 20.8 respectively. All others were active and their temperatures ranged from 20 to 36 but were concentrated in the range between 34 and 35. As shown in Figure 15 the lizards usually maintain body temperatures from 7 to 15 degrees above air temperature while active. By persistent basking they are often able to maintain sufficiently high body temperatures to be active even when environmental temperatures are much below the preferred level. They are able to initiate activities at body temperatures somewhat below 20 and under favorable conditions may then rapidly raise the body temperature by basking. At air temperatures of 16.2 (4 p.m. 19 April 1968) and 16.0 (ca. 9 a.m. 22 April 1968) lizards were found active, with body temperatures of 31.5 and 32.6 respectively.

Reproductive cycle. Viviparity in *S. malachiticus* is seemingly correlated with its occurrence at medium to high altitudes. The gestation period has not been recorded, but is believed to be as much as four months. Perhaps it is considerably longer at the highest altitudes where the lizards occur. Viviparity limits the frequency of reproduction, and perhaps the number of young per brood. Plate III (lower) illustrates relative sizes of a female and her newborn young.

Marion and Sexton (1971) discussed the reproductive cycle of *S. malachiticus* as revealed by 10 collections averaging about 10 individuals each, obtained in central Costa Rica at various times of the year. Most adult females from mid-January to early April contained only nonyolked follicles. Yolked follicles were found only in late June (July, August and September were missing from the records), and embryos were present in most of those examined from early October to late January. The authors concluded that growth of ovarian follicles occurs through June, July and August and ovulation occurs in early September. Males seemed to be in breeding condition (testes at maximum size and an abundance of mature sperm in the epididymes) only in June. In March and April testes were undergoing progressive enlargement and some had mature sperm, but sperm was not yet present in the epididymes.

My data from the Cartago study area correspond fairly well with the annual cycle described by Marion and Sexton. Population samples in late 1967 and 1968 showed the following trends.

1 Nov.	Only adults and subadults present; most females obviously gravid.
10 Dec.	Newborn young and some large enough to be nearly a month old present along with adults; larger young absent.
14 and 21 Jan.	Young from newborn size up to 40 mm make up a large part of the population, which otherwise consists of adults.
6 March	Young, from those recently born up to 52 mm make up the greater part of the population.
22 and 28 April and 5 May	Population has a high proportion of partly grown young with dividing line between young and adults no longer sharply defined.
6 and 16 June	Population consists mainly of large young and adolescents.
11 Aug.	Recently matured adults and large young make up most of population.
1 Sept.	Population consists essentially of adults, with a few well-grown young.

In an earlier study of the reproduction of *S. malachiticus* in Costa Rica (Fitch 1970:45) I suggested the possibility that females might produce more than one litter annually because, in a pooled sample representing various localities and altitudes, there were young indicating occurrence of births at almost all times of year. Samples from high altitudes, especially, do not conform well with the seasonal trends postulated by Marion and Sexton and shown by my records from Cartago. Table 6 shows the occurrences of gravid females and young in five series totaling 89 specimens collected at high altitudes. The first two series show that there are many births in December, January and February. The remaining three series (KU) were collected at the opposite time of year and show that at high altitudes there are also many births in May through August—perhaps as many as in the winter months.

Under the climatic regime of Cartago sexual maturity is attained within six months of birth. One female caught and marked soon after birth (33 mm) on 1 Jan. had grown to 64 mm on 16 June, and another perhaps born in early February and marked on 28 April (48 mm) was gravid when recaptured 11 Aug. (length 64). Both were typical of their population in growth and probably produced young late in their first year of life.

At higher altitudes activity is limited by low air temperature, clouds and mist, and both gestation and growth must be retarded. As a result, attainment of maturity is probably delayed, and young born in February might not produce their own litters until the second summer at an age of around 18 months. The 36 young from high altitudes in the February, July and August collections seem to represent births in the months January, February, and April through August. On 24 Oct. 1967 near Vara Blanca, 1800 m, a juvenile of about 40 mm was seen, probably representing an August birth. The evidence strongly suggests that at high altitudes births occur throughout the year, with partial or complete breakdown of the seasonal schedule prevailing at lower elevations because individuals are unable to mature in time to produce litters at the age of one year. In general, montane lizards are longer lived than their lowland relatives,

TABLE 6. Seasonal occurrence of gravid females and recently born young in *Sceloporus malachiticus* from high altitudes.

				Young	
Locality	Date	Number in sample	Gravid females lengths	Length	Estimated age in months
Río Cotón and R. Cotó Brus, 1500-1800 m	mid-Feb. 1965	26	60, 61, 65, 68 70, 72, 75, 76, 79 83, 90	28, 30, 30, 31, 33 38, 39, 41 48	< 1 1.5 2.5
Volcán Barba, 2100 m	10-21 Feb. 1965	9	70, 73	31, 33 39, 41	< 1 1.5
Volcán Irazú, 2900-3100 m	3-5 July 1947	15	63, 64, 66 70, 74	32, 35 40, 40, 44 48	< 1 2 2.5
Volcán Barba	11-17 July 1951	11	69 76	31	< 1
Volcán Barba, 1860 m; and Cerro de la Muerte	9-10 Aug. 1951	28	68, 70, 71	33, 35, 35, 36, 36, 37, 38 41, 42, 43, 44, 45, 45, 48	0.5-1.5 1.5-2.5

and have lower reproductive potentials (Stebbins and Robinson, 1946; Fitch, 1972). The effect of altitude on reproductive effort (including time required to reach maturity, number of young in litter, frequency of litters and size of young at birth) needs to be studied in *S. malachiticus*.

Sceloporus squamosus Bocourt

Description. Small, with fine keeled scales; limbs relatively short, body slender, tail attenuate (more than twice length); head reddish brown, dorsal coloration brown with pale dorsolateral stripes; ventral coloration dull white, with no trace of bright display colors characteristic of most other members of the genus, in males at least; sexes essentially alike in size, coloration and markings (Plate III, upper).

Range and habitat. Occurs from Chiapas southeast at low and moderate elevations to northwestern Costa Rica on Pacific versant, and extends into dry valleys of Caribbean versant in Guatemala and Honduras. The lizards are mainly terrestrial, sometimes climbing on boulders, low bushes, or the bases of trees. The habitat is in relatively open situations where vegetation is sparse and there are intervening patches of bare ground.

General habits. Only a dozen of these lizards were seen in the course of my field work in Costa Rica. They were found at Playas del Coco, Sardinal, near Liberia (28 km east northeast of Sardinal) and at two intermediate localities. All were in open, disturbed situations, such as nearly barren fields grazed by horses and cattle, or roads or trails. The lizards were not wary. When flushed they ran only a meter or two at a time, and were captured with relative ease compared with *S. variabilis* and especially *S. malachiticus*.

Sceloporus variabilis Wiegmann

Description. Medium small, stout-bodied, having fine keeled and mucronate scales; tail usually 1.3-1.5 times length; color dorsally tan with dark brown blotches (about 12 pairs from nape to base of tail), each blotch having a smaller, whitish area on its posterior side; blotches continue onto tail where they tend to form chevrons (proximally) or faint rings (distally); dark dorsal blotches obscure or indiscernible in adult males but with their whitish posterior portions emphasized, and a pair of dull whitish dorsolateral stripes developed; sides darker than dorsum; dark spot on each shoulder, sometimes obscure, limbs and toes with faint dark bars; large, paired ventral patches of bright blue and rose in adult males (faint in immature males, absent in females and hatchlings); pair of large indented and well differentiated postanal scales in males; 7 to 12 femoral pores. (See Plate III, middle.)

Range and habitat. Occurs from Tamaulipas in northeastern México south into Central America, mainly at low and intermediate altitudes, chiefly on the Pacific slope, to Puntarenas in Costa Rica. In Costa Rica it is limited to the relatively dry northwest.

Its habitat consists of dry, open ground with wood such as rough barked trees, logs, fence posts, or driftwood providing shelter and objects to climb upon. Sandy beaches with abundant driftwood and the dune groves adjacent to such beaches provide the best habitat and support the densest populations. Farther inland it is found in gullies and washes in rocky places, and on steep slopes—situations where ground vegetation is sparse.

General habits. S. variabilis maintains a high body temperature and spends much of its time basking. It does not emerge in the morning until sunshine has warmed its nighttime retreat, and upon emerging it moves into the open, finds a well insulated object such as a dry piece of wood against which to flatten itself to receive the

maximum solar radiation, and basks to raise the body temperature to the preferred level before beginning feeding, territorial activities or courtship. Compared with *S. malachiticus* it is less scansorial and spends a high proportion of its time on the ground.

Compared with other common species of the genus, *S. variabilis* is intermediate in degree of wariness. Depending on the situation and the individual, flushing distance of one approached by a person is usually between 3 and 6 m but may be less. One that is flushed does not seek shelter immediately but retreats to a more secure place. It may move only a few centimeters downward and to the opposite side of a fence post, or it may make a dash of 10 to 15 m to a clump of brush. If further pursued or disturbed, the lizard attempts to escape in any of several ways. Most frequently it enters a cavity or crevice in a tree trunk or fence post or it may climb high into a tree, even out onto small twigs; or it may suddenly burrow into the substrate of soft soil or sand with brisk lateral wriggling movements, then lie inert and fairly well concealed, even though the tail and top of the back may protrude. The burrowing usually occurs under the shelter of a grass clump or other screening vegetation, after the lizard has darted away from its pursuer, and the ruse is used especially in sandy situations where there are no better hiding places. The food consists of small insects and other arthropods.

Growth. A total of 285 records of growth were obtained from marked individuals. For 10 of those recaptured that were considered representative, gains in length were 25 to 40 to 47 to 55 in 75, 42 and 51 days; 25 to 35 to 43 to 48 to 53 to 54 in 75, 42, 51, 55 and 44; 25 to 36 to 44 to 50 to 54 in 96, 61, 42, and 47; 26 to 58 in 147; 27 to 59 in 173; 29 to 52 to 58 to 60 in 94, 98 and 32; 25 to 37 to 52 in 45 and 49; 28 to 44 to 57 in 93 and 55; 28 to 41 to 59 in 54 and 97; and 26 to 53 in 120. In this list the last two were males, all others were females.

For the first three months mean growth rate is approximately 5.5 mm per month; it slows to 4.4 mm per month in males and 2.9 mm per month in females for the second three-month period. Females may grow to minimum adult size in as little as four months from the time of hatching. Males grow a little faster at least in the later stages, and attain larger adult size (Table 3).

Spatial relationships. Figure 11 summarizes distances between captures after an average interval of several months in a large sample of *S. variabilis*. During the course of field work with these lizards I often learned to recognize individuals because of pecularities in their size or pattern or regenerated tail or because they were distinctly marked with paint. Typically, such individuals were seen time after time at the same station, and they obviously had an attachment for objects providing shelter. One that was stalked or chased sometimes made an escape dash or a series of dashes taking it as much as 24 m from the starting point, but usually the distance was much less. Normally, the lizard remained within a radius of a few meters, but it might temporarily shift its activities to outlying points where shelter was adequate, or might alternate between several points. Figure 11 shows that short movements—up to about 15 m—are most numerous, with 14% between 15 and 25 m and only a few exceeding 25 m. However, the maximum recorded movement was 690 m, and five lizards exceeded 600 m. How such long shifts may come about in a lizard ordinarily of such sedentary habits was demonstrated at Boca de Barranca when a spring tide occurred in the late afternoon of 14 April 1968. As piles of beach wrack were inundated, lizards ran confusedly in search of shelter or swam

frantically as they were swept away by the current. Massive piles of wrack were momentarily lifted, shifted and then allowed to resettle in a new position as each wave advanced and receded.

The recurring hazard to which beach lizards are subject was mollified in this instance by the fact that it took place in daylight and was not accompanied by high wind or rain. Other more devastating spring tides that were not actually witnessed took place during the course of the study and changed the configuration of the beach and the distribution of wrack on which lizards depended for shelter. In storms lizards clinging to floating debris, especially those in cavities of hollow logs or stumps, might survive a long time and might be carried for distances much greater than the 0.69 km recorded in the present instance.

Temperature relationships. These lizards are heliophilic, and during periods of activity body temperature is typically three to five degrees above air temperature (Fig. 19). Upon emerging from nighttime shelter, the lizard is nearly always well below its preferendum, and it basks in an exposed place until body temperature is elevated. In the tropical climate where the lizards occur, keeping sufficiently cool is often the chief problem. Then insolation is avoided and the lizards seek insulated shelters, or stay in the shade, with much reduced activity, so that they are much more difficult to find. As shown in Figure 19, body temperatures varied from 27.5 to 39.5 but were concentrated in the range 31 to 35. A preferendum in this range is characteristic of the genus *Sceloporus* and has been noted in many of the other species (Bogert, 1949; Brattstrom, 1965). Air temperatures at the times of capture ranged from 26.0 to 34.6 but were concentrated between 28 and 30.

Reproductive cycle. In 18 clutches I

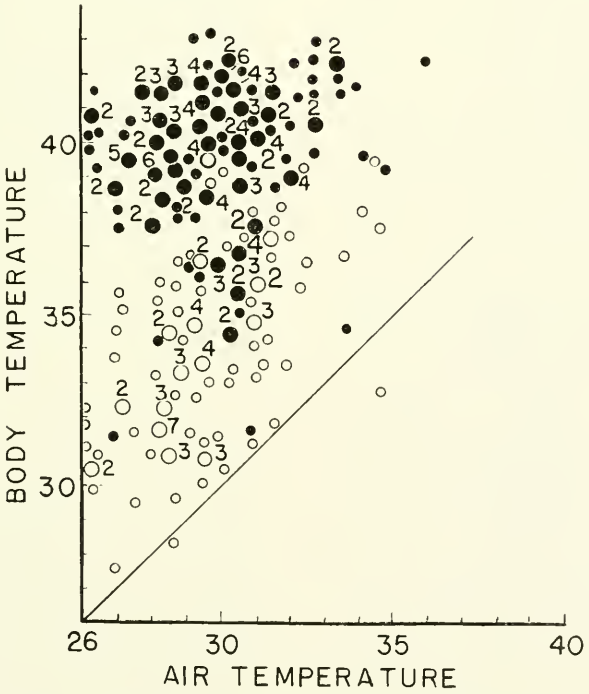

Fig. 19. Body temperatures and adjacent air temperatures of *Cnemidophorus deppii* (open circles) and *Sceloporus variabilis* (closed circles) from Playas del Coco and Boca de Barranca. Small and large circles show numbers as in Figure 10.

found an average of 3.0 eggs (1 to 5; Fitch, 1970:59). *S. variabilis* is thus one of the less prolific species of the genus, but living in the tropics in a climate that is mild throughout the year, it produces clutches frequently. Small young were found in each sample at both Boca de Barranca and Playas del Coco, but their numbers fluctuated greatly from one time of year to another indicating that productivity was at low ebb at some times and relatively high at others.

At Boca de Barranca, for instance, in November and December of 1967 a large sample was rather uniformly divided among lizards of many size groups, from hatchlings to large adults, showing that reproduction had been occurring at a high level for several months previously. However, in February young had become relatively scarce and in early April and the end of June the population consisted almost entirely of adults. In late August, both in 1968 and 1969, the population had a high proportion of hatchlings and few young of intermediate size, showing that a new period of increased reproductive activity was underway after a long period of relative quiescense. During most of January, February, March and April there were no gravid females, but some became gravid in May and from then through November a substantial portion of the females were gravid (Table 7). Hatching reached a high level in July and continued high through November, tapering off in December.

TABLE 7. Percentage of month-to-month samples of adult female *Sceloporus variabilis* that were gravid.

Season of sample	Boca de Barranca		Playas del Coco	
	N	% gravid	N	% gravid
Nov. 1967	6	16	12	0
Dec.-Jan. 1967-68	17	6	10	0
Feb.-March 1968	34	0	24	0
April 1968	31	0	....	....
May 1968	25	40	34	30
June-July 1968	28	29	37	16
Aug. 1968	20	55	11	45
Feb. 1969	34	24	15	33
Aug. 1969	26	42	19	53
Feb. 1970	23	13	18	17

TABLE 8. Months of hatching of *Sceloporus variabilis* extrapolated from sizes of young in each sample.

	Playas del Coco (N=236) % of year-round sample	*Boca de Barranca* (N=232) % of year-round sample
Jan.	3.0	1.7
Feb.	5.1	3.0
March	3.4	....
April	5.5	.9
May	.9	.4
June	1.8	3.5
July	11.0	12.9
Aug.	10.6	26.3
Sept.	14.0	17.3
Oct.	13.2	15.1
Nov.	22.4	15.1
Dec.	9.3	3.9
Total	100.0	100.0

The trends of seasonal cycles at Boca de Barranca and Playas del Coco are similar in most respects (Fig. 13), but the November-to-May lull in breeding is more complete at Boca de Barranca (Table 8).

Family **Anguidae**

This almost cosmopolitan family has few representatives in Costa Rica and is not prominent ecologically.

Gerrhonotus monticola Cope

Description. Medium-sized, elongate with short, pentadactyl limbs and heavy cylindrical tail; deep lateral fold with granular scales from behind ear to groin; dorsal body scales in 16 longitudinal rows, rhomboidal, keeled except in nuchal region; ventral scales smooth, in 12 longitudinal rows; in most females and in young dorsal color is pale brown with a series of middorsal black spots, sides darker

with occasional white flecks; adult males often heavily pigmented, mostly black, speckled with many light colored greenish-yellow flecks or spots which have some tendency to align themselves longitudinally in broken streaks along the body; ventral surface dull gray with dark pigment concentrated in the middle of each longitudinal scale row forming faint longitudinal lines.

Range and habitat. Occurs at high altitudes in Costa Rica from at least as far north as Volcán Poas southeastward through the Cordillera Central and Cordillera de Talamanca into Chiriquí in Panamá. Inhabits cloud forest, forest edge and sometimes brush or pastureland or vicinity of buildings, sheds, corrals, or rock piles. It is usually dependent on dead wood such as stumps or logs with loose bark, boards or woodpiles.

Reproductive cycle. A series of 38 (KU) from Volcán Irazú, Volcán Barba and Vara Blanca in July consists of three indistinct size groups: 1) juveniles 30, 36, 41 and 52 mm in length, judged to represent births in June, May, April and January, respectively; 2) 11 adolescents (including two gravid females) 58 to 65 mm in length and judged to be 8 to 10 months old; 3) 23 adults 68 to 86 mm in length, of which all ten females are gravid. Nine females have follicles 2 to 6 mm in diameter, and the two largest have uterine eggs recently ovulated. From analogy with the closely related *G. coeruleus,* similar in size and living at similar temperatures in the coastal region of the northwestern United States, it is suspected that gestation in *G. monticola* lasts from seven to ten weeks. A concentration of births in October and November could be expected from the females having enlarging follicles in July; most of these females would have required several weeks for their ova to mature before conception.

Three series of specimens (KU) from Cerro de la Muerte were studied. Sixteen in August included one recently born young, one female with nearly full term embryos, four nongravid females that may have given birth recently, one female with recently ovulated eggs and two with enlarged follicles. In this series the adolescents are poorly represented, and the adult females seem somewhat accelerated in the timing of their breeding compared with those discussed in the previous paragraph. A June sample has one female with large follicles, one with uterine eggs, and a 56 mm adolescent perhaps born in November. A February-March sample has two adult nongravid females, a 34 mm juvenile perhaps born in January, and a 55 mm adolescent perhaps born in August.

At Hacienda El Prado in November 1967, I captured a gravid female and a 46 mm juvenile, perhaps born in July.

The combined evidence from occurence of gravid females and of juveniles suggests that births are concentrated in October and November, but occur in smaller numbers throughout the remainder of the year. Females probably mature in time to produce first litters at an age of approximately one year.

Family **Teiidae**

This large family of the Neotropical region and southern North America is well represented in Costa Rica. Three species of *Ameiva* and one of *Cnemidophorus* were included in my study. These are medium-large, active, terrestrial lizards occurring in high population densities and playing an important role as predators on arthropods, as competitors of other insectivorous animals and as a food source for larger predators. *Ameiva* and *Cnemidophorus,* considered congeneric by some authorities, are somewhat different ecologically, *Ameiva* occurring in various types of forest and *Cnemidophorus* in more open, xeric situations. There is over-

lap. In many localities in northwestern Costa Rica, *A. undulata* and *C. deppii* occur in the same habitat and seem to be competitors for food and space, but on the average *C. deppii* is in more open situations. Potential competition is even greater between *C. deppii* and *A. quadrilineata,* which often are beach lizards, remarkably similar in habits and habitat. *A. quadrilineata* occurs as far north as Quepos and *C. deppii* as far south as Boca de Barranca, but it has not been determined whether their ranges meet or how the transition occurs in the 90 km interval between Barranca and Quepos. At Portéte, *A. quadrilineata* and *A. festiva* occurred together, but the latter was much scarcer and much more closely limited to dense vegetation. At Quepos both *A. quadrilineata* and its near relative *A. undulata* were present, but the latter was confined to leaf litter and undergrowth in forests and plantations.

Ameiva festiva (Lichtenstein)

Description. Large, stout, with long, pointed snout, moderately long tail, and powerful legs; scales are fine and granular on dorsum and sides, but on ventral surface are large, smooth plates, in eight rows (six anteriorly); tail with enlarged, heavily keeled, spiny scales in regular whorls; color dark brown with a pale (yellow or greenish or bluish) middorsal narrow stripe extending from the tip of the snout posteriorly along the body and tail, where it becomes obscure, irregular with indented margin on body; a pair of broad lateral black stripes on body; one or more dorsolateral series of cream-colored, bluish-tinted, irregularly shaped spots and streaks between pale dorsal stripe and black lateral stripe, or encroaching on the latter; ventral surface dull white or with reddish or greenish suffusion of throat in male; tail bright blue in hatchling, gradually fading to brown in older lizards.

Range and habitat. Occurs from México at the Isthmus of Tehuantepec south and east through Central America, and in Colombia, South America, chiefly in humid tropical lowlands; absent from northwestern quarter of Costa Rica, where there is a pronounced dry season, but present on Pacific slope in humid southwest *(A. f. occidentalis);* occurs to at least 600 m in subtropical zone (Turrialba). It is primarily a forest lizard, but requires basking places with sunshine, and it thrives in seral situations such as provided by plantations of banana or cacao. It is present on the coast in coconut plantations, and on the beach, but in these places it is much less numerous than *A. quadrilineata* and tends to stay in or near cover such as hedges or thickets.

General habits. A. festiva is a highly mobile terrestrial lizard, which maintains a high body temperature by basking, and travels with rapid jerky movements, finding arthropod prey by visual, tactile and olfactory sense, with almost constant probing or digging while active. Yet it spends a relatively large part of its time inactive under shelter. Even when weather conditions are optimum, the lizards emerge late in the morning and retire early in the afternoon. When the sky is overcast or rain is falling, they do not emerge. At Pandora, Smith (1968) noted that throughout rainy periods, often lasting for a week or more, they kept to their shelters and were not seen in the banana groves.

Even when actively foraging, these lizards spend long periods within a few square meters, moving around the same log or pile of debris. After being chased into cover, one might be found after a few minutes back at the original location. A home range is probably comparable to one of *A. quadrilineata,* or even smaller.

Growth. Only one record of growth was obtained; a female at Portéte marked 9 May 1968, when she was 69 mm in

length, was recaptured on 12 June, grown to 81 mm, and gravid. Such rapid gain indicates that *A. festiva* grows and matures at least as fast as *A. undulata* and *A. quadrilineata*, and most individuals probably reach sexual maturity between three and six months after hatching.

A puzzling aspect of Smith's (1968) findings concerns the small average and maximum sizes that he indicated. In his 1963 sample of 225, he stated that males ranged from 39 to 100 mm ($\bar{x}$=67.6) and females from 37 to 94 ($\bar{x}$=70.0). Many adults of both sexes that I examined exceeded 100 mm. Two gravid females that I collected at Pandora on 11 March 1965 had lengths of 82 and 104.

Reproductive cycle. Smith (1968) concluded that there was no seasonal variation, since all mature females, regardless of the month they were collected, contained yolked follicles or oviducal eggs and/or corpora lutea. However, the 81 gravid females that he recorded were chiefly from late July, August and early September, and evidently the samples from other months were small. From experimental females, Smith determined that the interval between the initiation of deuteroplasmic activity in a set of follicles and their ovulation is approximately eight weeks, and egg-laying occurs after another three weeks or a little less. Hence a total of nearly three months is required for production of a clutch. Smith estimated that a female would produce an average of at least three clutches annually. In this he was conservative, as there is ample time for production of four clutches if the 11-week period for production of a clutch, and the lack of any pause between successive clutches as Smith observed, are accepted as the rule.

A sample of 91 *A. festiva* (KU) from a dozen Costa Rica localities but mostly from Los Diamantes, Turrialba, Suretka and Tenorio, were collected in March (7), July (31), August (31) and September (22). For these 4 months gravid females made up 29, 19, 13 and 32% of the samples, respectively; young in their first month made up 43, 16, 16 and 23%, and supposed second-month young made up 0, 19, 10 and 9%. Supposed third-month young made up 6% in July and 19% in August. Arbitrary age estimates were made as follows: first month, 41 to 55 mm, second month, 57 to 69 mm, third month, 70 to 80 mm. Sight records of 50 from Portéte are as follows: January (6): hatchlings 33%, second-month young 17%; March (8): hatchlings 25%, second-month young 37%; May-June (6): hatchlings 16%, second-month young 16%, third-month young 50%; late August-early September (26): hatchlings 15%, second-month young 8%; October (4): all large young and adults. The trend of the records tends to bear out Smith's contention that there is year-round breeding but the samples are too small to show significant differences between months.

Ameiva quadrilineata (Hallowell)

Description. Stout-bodied, similar in most respects to *A. undulata* but markedly smaller; distinctive in having a broad black, dorsolateral stripe on each side; brown middorsal area has pale lateral edges where it contacts black dorsolateral stripes; this dark stripe is bordered below by a narrow white stripe extending from temple to groin; below the white stripe sides are spotted with white; throat yellowish in male. There is only one loreal on each side. Sexual difference in size is slight. Pattern remains distinct in adults but it is more sharply defined in the juvenile, which has a bright blue tail.

Range and habitat. Humid lowlands of Costa Rica on both coasts. On the Pacific Coast it extends north only slightly beyond Quepos. On the Atlantic it occurs from Nicaragua to Panamá. It extends

far inland (Suretka, Limón Province and San Isidro del General, San José Province) in humid forest but also is a typical beach lizard and in both the localities where I observed it the species was limited to beaches and nearby areas. Although in both areas its population density was high on the beach, it did not seem to extend much more than 100 m inland. At Tortuguero, Hirth (1963a) found *A. quadrilineata* in all zones of the strand, but most abundant in open sunny areas under coconut trees.

At Portéte I observed these lizards mainly in a coconut grove, where there were broken patches of sunlight and abundant shelter including jagged coral rock, logs and sticks, dried palm leaves, piles of coconut husks, and in places a dense mat of ground vegetation. At Quepos the lizards were far more abundant and were found over a wider range of habitats. They were found even on the open sandy beach where there was no growing vegetation but where tidal wrack provided abundant shelter. They were most numerous in coconut groves, but were present also in plantations of bananas and other arborescent crops, and often retreated into the tangled vegetation at the edge of a mangrove swamp on the leeward side of the front dune.

General habits. As a heliotherm *A. quadrilineata* requires sunshine and open areas. Its usual habitat is much more open than that of its near relative, *A. undulata*, and it is less shy and secretive. With slow and cautious movements an observer can often approach within a meter or two. However, it cannot be easily herded or driven like the more active *Cnemidophorus deppii*. An attempt to catch one in this way nearly always resulted in the lizard becoming increasingly wary and finally hiding in a burrow or beneath some object. If routed from such shelter, it would immediately scramble to a new hiding place.

These lizards travel with brisk, jerky movements and obtain their prey by active search. Much time is spent in digging and probing, and seemingly much of the prey is found by olfaction. In the stomachs of 244 *A. quadrilineata* that Hirth (1963a) examined at Tortuguero, talitrid amphipods, tenebrionid beetles and lycosid spiders were by far the most important foods.

When active, *A. quadrilineata* has the high body temperature and high metabolism characertistic of teiids, but it spends relatively little time in activity above ground, emerging only after the sun has warmed the soil and air, and sometimes retiring again to shelter about midday. In the rainy season, in cloudy or inclement weather, it may not emerge at all for periods of days. At Tortuguero, Hirth found population densities of 12 to 26 per acre with adults generally more abundant than juveniles.

Growth. From 32 recaptures, Hirth (1963a) found that beyond 40 mm males grow faster than females, with a slowing trend in both sexes. From his figures the correlation between age and size in Table 3 is tentatively suggested. The smallest female with oviducal eggs found by Hirth was only 48 mm and hence might have been only two months old, but most fecund females are probably more than four months old.

Spatial relationships. At Tortuguero, Hirth (1963a) found home ranges of the following average dimensions in square meters: adult male 445, adult female 188, juvenile male 269, juvenile female 227. He found that adult males roam more or less randomly throughout the home range, but adult females have strongly defined centers of activity, usually a favorite log. Juveniles have less strongly defined centers of activity. Hirth had less data for the dry season in March and April than for the

remainder of the year, but he found some indication that home range size was reduced in the dry season, because of high temperature of the sand surface inhibiting movement in open situations, and lack of the tidal debris that attracted the lizards at other times.

Turner, Jennrich and Weintraub (1969) suggested that home ranges plotted from minimum polygons are nearly always smaller than actual ranges, and they proposed a correction factor based upon the number of records used in plotting the area. Applying their correction factor to Hirth's figures, Turner *et al.* calculated an average home range of 1045 m^2 for adult males and 417 m^2 for adult females.

In my field work an impression of extremely small home ranges such as found by Hirth was gained from repeatedly observing what seemed to be the same individuals at approximately the same places. I did not notice the tendency for females to have more strongly defined centers of activity.

Temperature relationships. Hirth (1963a) obtained 698 body temperatures at Tortuguero, with corresponding air temperature and substrate temperature for each. The histogram from these records, arranged on a half-degree scale, showed a typical skewed curve with greatest frequency at 37.5 degrees. Hirth suggested the following thermal categories for *A. quadrilineata:* ecological optimum, 37.6 (± .06); normal activity range, 34.6-40.0; basking range, 27.6-34.5; minimum voluntary tolerance, 24.0-27.5; critical maximum, 45.1 (± .17). Hirth's histogram shows that activity is greatest when air temperatures are in the neighborhood of 29 to 30, and 32.5 seemed to be the optimum substrate temperature. The lizards maintain their temperatures within their preferred range by active movements—to heated sand and sunlit places when body temperature is too low and to shaded damp places or beneath objects when body temperature is too high.

Reproductive cycle. Hirth (1963a) stated that at Tortuguero "During the mating season, the flanks of most males become greenish-blue . . ." His field observations were made during the period of June to September in two different years, but he believed that the peak of egg-laying was in May and June, and young were present in greatest numbers in August and September. However, young were present also in June, July, and January through April, and according to the reports of some residents of the area, they were present year-round.

At Pandora, about 30 km south of the site of my study at Limón and 110 km southeast of Tortuguero, Smith (1968) found that all mature females, regardless of the month they were collected, contained yolked follicles, or oviducal eggs and/or corporea lutea. He therefore concluded that they were reproductively active throughout the year, but most of the lizards were collected between 15 July and 11 Sept. Relatively few were collected at two-week intervals between 1 Oct. 1965 and 31 May 1966. Smith's field work was done in banana plantations, and he emphasized the homogeneous nature of the cover and the heavy year-round rainfall.

My observations were made chiefly at Quepos, in a hotter and sometimes drier climate than at Pandora or Tortuguero. Nevertheless, at each sampling there seemed to be some gravid females, and there were always hatchlings or young near hatchling size. For specific dates the percentage of the population consisting of young estimated to be less than a month old were as follows: 14 Dec. 1967—22; 17 Jan. 1968—37; 24 Feb. 1970—13; 7 March 1969—24; 1 May 1968—10; 20 June 1968—7; 21 Aug. 1968—22; 25 Aug. 1969—7. The high percentage of young in mid-January seems to indicate peak production of eggs

in late October, with other high points indicated in mid-December, early May and late September (Fig. 9). October corresponds with the peak of the rainy season, and it seems that in general a high level of egg-laying is correlated with heavy precipitation. Nevertheless, production continues at somewhat depressed levels through the dry season.

Ameiva undulata (Wiegmann)

Description. Medium-sized, heavy-bodied, long-toed, long-nosed, long-tailed, with fine, granular scales dorsally on the body, and large scales on the ventral surface and tail; color dull, predominantly tan, with black marks on the sides (Plate IV, upper); salmon-colored suffusion on chin, throat and chest in breeding males; young longitudinally striped on body, with blue tails.

Range and habitat. A. undulata has 12 recognized subspecies, with a range that extends from southern México, on both coasts, south through Guanacaste Province of northwestern Costa Rica, and as far as Quepos, Puntarenas Province, on the southern coast. It occurs mainly in lowlands, but in Costa Rica encroaches onto the Meseta Central as far as the western outskirts of San José.

The habitat is leaf litter in open type of woodland, or woodland edge, or situations near to woodland. In the course of my field work these lizards were found in xeric scrub and brush, in lowland swamp forest, gravelly edges of streams, in cafetal, banana groves, pineapple plantations, fields, pastures, along railroad tracks and roads, and in suburban yards and vacant lots.

General habits. A. undulata is a strictly terrestrial lizard which finds its prey by active search, guided by visual, tactile and olfactory sense. It moves about with a quick, jerky gait, digging, probing and nosing in niches, holes and crevices for arthropod prey including pupae and eggs. In the course of its normal activities the lizard changes direction frequently so that in travelling only a few meters it crosses its own trail several times without progressing much farther from the starting point, and without venturing far from a potential refuge.

The lizards are heliotherms that maintain extraordinarily high body temperatures and are active only when the sun is shining or has been shining recently. Even at the times of year when they are most active the lizards spend only a few hours a day above ground and remain concealed and quiescent most of the time. At some times of year adults are not in evidence and perhaps spend periods of days or weeks inactive without emerging.

One that is followed tends to keep near a hiding place except when it makes an occasional dash across open ground from one thicket or log to another. One that is active may be readily approached to a distance of 3 m or even 2 m by a person moving slowly and cautiously. The lizard may even move up to or in contact with the feet of a person standing in the vicinity, but any sudden movement will send it scurrying for shelter. If an observer moves cautiously following the lizard, the latter continues its activities but tends to maintain or increase the distance between it and the person, and to keep a barrier such as a log or bush between. At any further alarm it makes a short and rapid dash for shelter, and hides beneath a log, in a burrow or merely beneath the leaf litter. If there is no further disturbance, the lizard may emerge slowly and cautiously after a long pause to look about warily with only its head protruding. Having emerged from shelter, the lizard may lie quietly, watching, while a person moves about in the vicinity. A lizard that has escaped into leaf litter may move beneath the leaves

and emerge a meter or more from the spot where it took shelter.

Growth. Twenty-nine marked *A. undulata* were recaptured a total of 49 times after periods of weeks or months and in every instance there was some growth. For 11 that are considered most representative, gains in length were 41 to 62 to 89 in 52 and 91 days, 50 to 57 in 14, 50 to 67 in 39, 52 to 85 in 99, 63 to 86 in 85, 65 to 86 in 35, 67 to 88 in 102, 69 to 98 in 148, 70 to 90 in 85, 70 to 89 in 144, and 74 to 96 in 104. The last individual was a male. Sex was not determined in the second and third; all others were females. The records of the first individual listed are especially significant in showing growth from the size of a hatchling to that of an adult in 143 days. For 3 young in the length range 40-60 mm gain per month was 12.0 mm, for 4 in the range 61-70 gain per month was 8.6, for 11 in the range 71-80 gain per month was 6.7 and for 15 in the range 81-100 gain per month was 5.8.

Spatial relationships. For the individuals recaptured the intervals between successive records averaged 39 days, and most movements were less than 20 m (Fig. 11), with 18% in the range 20-40 m. Stalking and catching the lizards often involved prolonged following and maneuvering, and the area covered during such a pursuit bore out the impression that home ranges with radii of approximately 12 m are typical. Adult males and females and young were much alike in their behavior, and in the extent of areas covered.

Temperature relationships. Activity is normally concentrated between 9 a.m. and noon. Body temperatures ranged from 29.6 to 40.5 (Fig. 17), but only one was below 33 and a third of the total were in the range 34-35, lower than in some other species of ameiva which live in more open habitat, (Fitch 1968). Most captures were made at air temperatures between 28 and 31.

Reproductive cycle. Percentages of adult females from Guanacaste that were gravid in different months were as follows: 42.9 of 7 in February, none of 4 in March, 31.5 of 13 in May, 63.5 of 11 in July, and 57.1 of 7 in August. The ratios of young to adults varied greatly in different seasonal samples. On 24 Dec. 1967, 20 km NE Finca Taboga, young of 45-50 mm, presumably between one and two months old, were abundant, but no other sizes could be found. On 18-19 March 1965 at Finca Taboga many young of 45-65 mm, probably from one to 2.5 months old, were seen, but no adults. Thus samples from December through March usually had a high proportion of immatures and few or sometimes no adults. However, the largest sample, obtained on 3 Feb. 1970 at Las Pavas, contained 72 lizards, with many adults and young of all sizes. The samples from April, May, July, August and September all contained a high proportion of adults including gravid females. Seemingly reproduction is at its lowest ebb in the early spring dry season, but is at its height immediately afterward, in April and May and the ensuing months, resulting in the production of a large crop of young about midsummer. Meanwhile the adult females continue to produce successive clutches of eggs at intervals of a few weeks, with the result that the total population and the proportion of young continues to increase until late fall. Reproduction is more inhibited by the dry season in the lowlands at La Irma (Fig. 18) than in the more equable climate of the Meseta Central at Las Pavas (Fig. 9).

At Sardinal a female of 79 mm contained three eggs, and a female of 87 mm contained two. Both were probably first clutches. Nine gravid females (KU) from the Yucatán Peninsula contained two to seven unlaid eggs. For the combined sample of 11 clutches, $\bar{x}=4.8$.

Cnemidophorus deppii Wiegmann

Description. Slender, medium-sized, long-tailed (more than twice length), long-nosed, long-toed, with fine granular scales dorsally on the body, large flat scales in 6 to 8 rows on ventral surface of body, and large keeled scales on tail; large scutes on anterior parts of fore- and hind-limbs, which have granular scales posteriorly; color predominantly brown dorsally with 7 thin longitudinal stripes, and dull white ventrally; in adult males dorsal surface is suffused with pale green on anterior parts, and ventral surface anteriorly is suffused with deep blue; tail bright blue in young, fading to gray in adult. (See Plate IV, upper middle.)

Range and habitat. C. deppii occurs on both coasts of México (northern Veracruz and Michoacán) southward into Honduras on the Atlantic slope and to southern Costa Rica between Puntarenas and Quepos on the Pacific slope.

In Costa Rica this species is prominent as a beach lizard. It occurs from the coast a few miles inland, but is found in greatest numbers in sandy situations with sparse vegetation, especially dunes of the ocean front. It often forages in beach wrack of the intertidal zone but is more at home on the upper beach where there are clumps of grass and patches of sea grape. Farther back from the beach it frequents groves, open woodland, scrub, and plantations, mainly in level sandy situations.

General habits. This is a terrestrial, diurnal lizard, the most active and agile of all the species studied, and gives an impression of haste and urgency as it moves about in a devious course, poking, probing and scratching for its arthropod prey. Correlated with this intensive activity is the lizard's high metabolism and maintenance of high body temperature, near 40. The lizards are active chiefly at times when the sun in shining. Emergence from nighttime shelter is noticeably later than in other lizards such as *Sceloporus variabilis* in the same areas. While temperatures are relatively low and sunshine is not intense, the lizards spend much of their time in sunlight, but as temperatures rise, they retreat to shaded situations and activity rapidly wanes during the heat of the day. Beyond midday few are active in the places where they were numerous during the morning hours. Hatchlings and other young sometimes continue their activity after adults have retired underground.

Like other species of racerunners that have been studied, these have remarkably small home ranges that can be traversed in an almost instantaneous dash. In addition to some open ground, each home range includes one or several shelters such as a log with holes inside or beneath, a trash pile, a thick bush, or a patch of low dense vegetation. At any suspicion of danger the lizard will move toward such a shelter, sometimes continuing to forage with no show of alarm. Seeming confident of its own speed and elusiveness, one may merely move away ahead of an approaching person, maintaining a separation of a few yards. If the person moves between the lizard and the nearest escape covert, the lizard often will change direction and cut back sharply with a sudden dash to reach the edge of the shelter, where it resumes more leisurely behavior. If cut off from such retreat it will make a longer dash to an alternative covert in a distant part of the home range. On the areas where the lizards were hunted, burrows of land crabs were numerous. A lizard that was cut off from shelter and hard pressed had only to duck into a burrow to escape. Sometimes a lizard made a long dash directly toward and into a crab burrow suggesting that the place was a habitual and well remembered refuge. On other occasions pursued and tiring lizards made rapid erratic searching movements over the ground surface for a second or more

before finding a burrow which may have been remembered inexactly or may have been located by chance. A lizard closely pursued or cut off from its intended shelter often changed direction with a sudden dodge and stopped with confusing suddenness, sometimes concealing itself beneath the ground surface or beneath a small object such as a stick or dried leaf.

Growth. A total of 124 marked racerunners were recaptured from one to four times after substantial intervals. Selected records for 13 that are considered representative follow. For 5 recaptured males, gains in length were 36 to 70 in 95 days; 41 to 74 in 92; 30 to 42 to 50 to 72 in 20, 55 and 94; 35 to 72 in 202; and 46 to 78 in 117. For 8 recaptured females, gains in length were 32 to 76 in 173 days; 39 to 77 in 154; 35 to 51 in 172; 35 to 61 in 167; 38 to 46 to 59 in 34 and 59; 34 to 46 to 54 in 128 and 49; 35 to 54 in 149; and 32 to 55 in 148. Most of these were marked while still in their first month and recaptured after growing to adult or adolescent size. They indicate that adult size may be attained in as little as four months but usually five to seven months are required. Males grow faster than females and are mature when they reach 70 mm; females are mature at a minimum length of 58 (Table 3).

Spatial relationships. Linear distances between capture sites were measured for 181 racerunners recaptured after several weeks or several months (Fig. 11). The distances ranged from 0 to 170 m but only 5 exceeded 60 m. In view of the ease and rapidity with which *Cnemidophorus* travels, most of the distances were remarkably small. Most were in the range 3 to 24 m (Fig. 11), with abrupt reduction in numbers for greater distances.

The short distances shifted by most individuals that were recaptured even after several months suggest that home ranges have some stability in time. At the Playas del Coco no. 1 study area, numerous juveniles were captured and marked in November and December 1967, but in the dry season few of them could be found and racerunners seemed to have become much scarcer. With the arrival of another rainy season, in May and June, racerunners were again much in evidence. Those present included many marked as juveniles in late autumn, but grown to adult size in the interval. These were consistently near their original capture sites, strongly suggesting that they had continued to live in their original ranges but perhaps with much reduced activity or actual dormancy for extended periods during the dry season.

Temperature relationships. A total of 189 body temperatures of active racerunners were obtained of which most were in the range between 39 and 42—higher than in any of the other lizard species studied, but within the range known to be characteristic of this genus in the Temperate Zone (Bogert, 1949; Fitch, 1956; Brattstrom, 1965). The active lizards had temperatures from 29.1 to 43.2 (Fig. 19). More were captured at air temperatures between 29 and 30 than in any other one-degree range, and numbers tapered off rapidly at higher and lower temperatures. Thus in the active lizards, body temperatures 9 to 12 degrees above air temperatures were typical (Fig. 19). The lowest air temperature at which an active racerunner was found was 26.1. At much lower air temperatures the lizards are too inactive to emerge and bask. The threshold of activity is therefore unusually high in this species. At the Boca de Barranca and Playas del Coco study areas racerunners emerged in the morning notably later than did other lizards such as *Sceloporus variabilis.* Greatest activity occurs at about midmorning, and by mid-afternoon it has virtually ceased.

Reproductive cycle. Noteworthy differences are evident in the seasonal trends

between the populations at Playas del Coco and at Boca de Barranca. The breeding season is much more restricted at Playas del Coco. There, in February 1968, 1969 and 1970, the population consisted mainly of adults and large young. In 1968 there were no hatchlings but in 1969 and 1970 hatchlings and other small young were well represented. In late March 1968 a sample of 34 had only one hatchling and five larger young. A late May 1968 sample of 119 had mostly adults but with one first-month young and four that were probably in their third month. Adult females were mostly gravid. A July 1968 sample of 89 consisted essentially of large adults, the females gravid, but there were two partly grown young. An early August 1968 sample of 107 had four hatchlings but otherwise consisted of adults and adolescents. A late August 1968 sample of 128 consisted mostly of adults and adolescents, but had 15 small young and three of intermediate size. A sample of 160 from the end of November and the first two days of December 1967 consisted mostly of young of all sizes with only three adults. A late December 1967 sample was similar, and both had many hatchlings. These samples show that egg-laying begins in the latter part of May, reaches a high level in June and remains high through October, then tapers off rapidly in November and December. Through the dry season, December to April inclusive, egg-laying is at low ebb but occurs occasionally, so that some hatchlings may be found at all times of year (Fig. 18). The July and August samples indicate a pause of about five months in reproduction.

At Boca de Barranca there is little or no reduction in the rate of egg-laying during the dry season. Samples from early January (51), early February (133), mid-February (99), late February (120), early April (211) and late May (105) all had many hatchlings and other young. Samples from late June to early July (89), and late August (191) had especially high ratios of hatchlings and juveniles. In all these population samples, the proportion of young less than three months old ranged from 17.6 to 50.5%. Hatchlings were least well represented in mid-November and early January samples, indicating some slackening of reproduction in September and October—the late rainy season.

There were obviously gravid females in each sample from both localities. In May through August samples the majority were gravid and obviously reproduction was at a high level at this time of year. In a series (KU) from Managua, Nicaragua (175 km NNW Playas del Coco) in late May and early June 1956, there were 11 females 60 mm or more in length, and all of them were gravid.

Eight of the females that were captured and marked at Playas del Coco and Boca de Barranca when they were noticeably distended with eggs were recaptured in gravid condition after intervals sufficiently long for them to have deposited the first clutch, 33, 34, 34, 35, 48, 49, 51 and 51 days. The female recaptured after a 35-day interval was less distended at the second capture than at the first, as was one of the females recaptured after 51 days. Eight others captured in nongravid condition appeared gravid when recaptured, after intervals of 34, 35, 41, 43, 50, 51, 54 and 58 days; three that were gravid at an early capture appeared nongravid after intervals of 34, 45 and 56 days. The female recaptured when nongravid after 34 days was unusually distended with eggs and obviously was nearly ready to produce a clutch at the time of her first capture, and she may have produced a second clutch before she was captured again. Obviously the intervals between successive clutches are somewhat variable. From the records cited above, and from analogy with the better known *C. sexlineatus* (Fitch, 1970:

97), I suspect that an interval of approximately 25 days may be typical.

Six clutches of eggs of *C. deppii* average 2.8, varying from one to four according to the size of the female. Females produce their first small clutches of eggs at 5 or 6 months, when they are still far short of average adult size and are growing rapidly. A female productive throughout the breeding season might produce about 17 eggs at Playas del Coco and somewhat more at Boca de Barranca if clutches are produced at approximately monthly intervals. Actually, neither the interval between clutches nor the incubation period are known, but perhaps both approximate those of the somewhat similar *C. sexlineatus* in the United States in which the interval between clutches is sometimes as little as three weeks, and incubation has been variously reported as 53 days in Oklahoma (Carpenter, 1960), 60 days in northern Kansas (Fitch, 1958a) and 61 days in North Carolina (Brown, 1956). In southern California, Bostic (1966) obtained evidence of a 50-55 day incubation in *C. hyperythrus*.

Family Scincidae

This cosmopolitan family is represented by few species in Costa Rica. *Scincella cherriei* is a small, abundant, oviparous, insect-eating species, usually in leaf litter of forests or plantations, and widely distributed in lowland areas in wet climates. *Mabuya mabouya* and *M. brachypoda* are medium-sized active, partly arboreal, viviparous lizards. They occur in relatively low population densities and have relatively low reproductive potentials.

Mabuya brachypoda Taylor

Description. Elongate, slender, similar to *M. mabouya* in most respects; limbs short, failing to meet when adpressed, separated by a wide gap; dorsum brown, almost uniform, with or without traces of dorsolateral stripes; a dark band on each side; scales usually in 30 (sometimes 28 or 32) longitudinal rows.

Range and habitat. Occurs from southern Guerrero south through the Pacific coastal region of southern México and Central America to southeastern Costa Rica. Its habitat requirements are similar to those of *M. mabouya* but it occurs in drier places.

Reproductive cycle. Two museum specimens (KU) from Boca de Barranca, 26 July and 21 Aug., each had 4 embryos about 18 mm in length. One from Tenorio, about 700 m elevation, on 21 Aug. had 4 small embryos. Webb (1958) and Davis and Dixon (1961) mentioned a total of 14 females in Michoacán and Guerrero, southern México, that had embryos in June or July, or produced litters in one of these months.

Mabuya mabouya (Lacépède)

Description. Medium-sized, slender, elongate, having small hexagonal polished scales usually in 26 to 30 longitudinal rows; a transparent disc in lower eyelid; limbs well developed, overlapping when adpressed; brown dorsally, with scattered black spots or dots and whitish markings, with a pair of narrow, cream-colored dorsolateral stripes and a similar pair of ventrolateral stripes and a wider dark area between.

Range and habitat. A remarkably widespread species occurring from Veracruz and Sinaloa in México south through Central America and the Amazon Basin in South America and on many West Indian islands including the lesser Antilles. In Costa Rica it occurs in both Caribbean and Pacific lowlands, and to altitudes of at least 800 m. Populations of the two versants are noticeably different; those of the Caribbean have frontonasal and rostral scales in contact, fewer (26-28) body scale rows, and better developed body stripes.

Taylor (1956) considered the two to be distinct species.

Although confined to hot climates, these skinks occur in a variety of habitats, both natural and disturbed—in rain forest, xeric woodland, banana plantations, coconut groves, rail fences, rock walls, and bridge abutments.

General habits. These skinks are secretive and wary; always found near shelter such as a hollow tree, crevice or burrow into which they escape at the slightest alarm, they are difficult to noose or catch by hand, and their population densities are usually low. Therefore, they are poorly represented in collections. They are largely terrestrial, but often are found on logs and tree trunks, and they climb well.

Like most other members of the genus, *M. mabouya* is viviparous. In this case viviparity is not associated with a cold climate, as it is with the other viviparous Costa Rican lizards studied—*Sceloporus malachiticus* and *Gerrhonotus monticola*. In the situations frequented by the skinks, eggs would usually be laid in burrows in shaded sites and so their incubation temperatures would be relatively low. Gravid females have the basking habit well developed.

Reproductive cycle. Fifty museum specimens (KU) were all collected in July and August. They consist of two poorly defined size groups—adults from 70 to 86 mm in length, and partly grown young. Ten of the twelve adult females are nonreproductive, but one from San Isidro del General on 22 Aug. has two follicles 3 mm in diameter, and one from La Lola on 10 Aug. has two nearly full-term embryos. Young make up about half the total sample and include specimens of 44, 49 and 50 mm, but 20 are concentrated in the narrow range 52 to 63 mm and might have all been born about the same time of year.

At Portéte on 4 March 1969 I captured a female distended with large embryos, and at Pandora on 11 March 1965 I captured one that had a single full-term embryo. These two records suggest that births may be concentrated in March. The lack of small young among the museum specimens collected in July and August, and the high proportion among them of young somewhat more than half-grown, sizes that might be reached at an age of four or five months, support this idea. It is tentatively concluded that in Costa Rica births are concentrated in March, but with some at the opposite time of year and perhaps throughout the entire year. The growth rate implied by this schedule indicates that young mature and conceive in time to produce litters when they are one year old.

Scincella cherriei (Cope)

Description. Small, elongate, bronze-colored with shiny scales, a long, heavy tail, and small pentadactyl limbs, the adpressed forelimb and hind limb overlap widely in juveniles and slightly in most adult males, but do not meet in large adult females; there are 30 or 32 scale rows around the body and 62 to 69 scales from occiput to vent; an irregular dark stripe behind eye extends along neck, obscure posteriorly; sides darker, dotted with black and tan, ventral surface yellowish, undersurface of tail gray, lower eyelid with transparent disc in center.

Range and habitat. S. cherriei occurs throughout much of Central America, from Tabasco, México, to Panamá, with four subspecies. In general it is limited to lowlands or intermediate elevations, and to humid climates. It is abundant in the eastern lowlands of Costa Rica, but relatively uncommon on the Pacific slope and perhaps absent from extensive areas of arid climate in Guanacaste in the northwestern part of the country.

The habitat is the forest floor of tropical rain forest, and forest edge, and in a

variety of disturbed situations. Many of those seen in this study were in cacao groves. Others were in low grassy and herbaceous vegetation in open woodland or scattered groves. Leaf litter is the most frequent shelter.

General habits. These skinks are furtive and secretive, usually remaining under cover. They sometimes emerge for brief periods of basking, but with part of the body or tail still concealed beneath a leaf or stem. Much of their activity takes place beneath the concealment of low vegetation or leaf litter; seemingly the food is found largely by olfaction. The lizards are strictly diurnal and limit their activity to relatively brief periods when humidity is high and temperature is moderate. Especially in midday heat of sunny weather, they are inactive, and in the cool of the morning do not show themselves until sunlight warms their hiding places. At any alarm the skink darts out of sight into a hole or crevice or beneath debris or surface litter. If the hiding place is superficial, trampling or turning of objects may cause the skink to show itself a second time in a dash for more secure shelter. Hiding places seem to be numerous and the escaping skink disappears after a dash of at most a meter or two.

Growth. For 12 recaptured, gains in length, all within the period 12 Nov. 1967 to 8 May 1968, were 25 to 31 in 77 days, 36 to 51 in 117, 35 to 52 in 177, 37 to 43 to 47 in 75 and 41, 43 to 51 in 77, 47 to 51 in 81, 48 to 53 in 116, 48 to 53 in 82, 49 to 54 in 77, 51 to 58 in 78, 52 to 57 in 117, and 53.5 to 56 in 117. It is noteworthy that each one recaptured had made substantial gain in length, although some were already in the size range of adults when they were marked. The tentative age-length correlation in Table 3 is based in part upon extrapolation from Brooks' (1967) growth curve for *S. laterale* showing the most rapid growth in the first month of life, since all the marked young of *S. cherriei* that I recaptured were more than a month old at the time of marking.

Spatial relationships. A total of 46 were recaptured after an average interval of 54 days. The longest movements (40, 38, 36.5, 35, 30, 27 and 27 m) were all made by females and, even excluding these records, the average distance for 23 females, 10.6 m, was a little larger than the average for 17 males, 9.7 m, indicating that females are the more vagile. Nearly half the recorded movements were in the range 6 to 12 m, and relatively few exceeded 21 m (Fig. 11), indicating that the usual home range is within an area of this diameter.

Temperature relationships. Body temperatures of these skinks were recorded from 22.5 to 31.0 with records especially concentrated in the range 25-27 (Fig. 14). For a tropical lizard this skink has a low temperature preferendum, but its body temperatures resemble those of the North American skinks that have been studied most *(Eumeces fasciatus, Scincella laterale)*. Body temperature tended to be the same as air temperature or only a little higher, thus these skinks are not heliotherms. Occasionally they have been observed basking in sunshine, but usually only briefly and with only part of the body exposed. Most captures were made in the range between 23 and 27 of air temperature. Ground skinks were found throughout the hours of daylight, but with definite peaks at mid-morning and mid-afternoon.

Reproductive cycle. Trends in reproductive status of the skinks at the Turrialba study area are shown by the following sequence of visits from November 1967 to February 1969.

12-16 Nov.: Sample of 50 included juveniles in first month (1), second month (2), and third month (3), and 21 adult females, only one of which was judged to be gravid on

the basis of external appearance. Three others dissected had only minute ovarian follicles.

28-29 Jan.: Sample of 47 included juveniles in second month (1) and third month (1), and 20 adult females of which 6 were judged to be possibly gravid.

8-10 Mar.: Sample of 65 included no small juveniles and one of third-month size (perhaps from an egg laid in November), and 34 adult females, most judged to be gravid; two of these were dissected and one had large uterine eggs and the other had medium-small (3 mm diameter) ovarian follicles.

20 Apr.: Sample of 32 included no juveniles less than three months old and consisted mostly of adults of which 14 were females. At least four of these were nearly ready to lay and shelled ova were discernible through the body wall.

8 May.: Sample of 22 included second-month young (3) and third-month young (2), and seven adult females of which four were judged gravid and one of these had uterine eggs visible through the body wall; another of the four dissected had recently ovulated eggs.

13 Aug.: Sample of 24 had first-month (1), second-month (3) and third-month juveniles, and eight adult females, all but one of which appeared gravid. Two that were dissected had medium large ovarian follicles (3 mm and 4 mm in diameter).

20-21 Feb.: Sample of 24 had only adults; a large number escaped, and all these were adults too. Of the 13 females, two had undeveloped gonads and 11 had ovarian follicles, mostly in early stages of growth, but up to a maximum diameter of 7 mm.

Although most of the Turrialba samples were small, they indicate seasonal change in the level of reproductive activity (Fig. 8). In November a breeding season is ending, most females do not contain developing eggs and the population has a high proportion of young from adolescent size down to hatchlings. In December through March, egg-laying and hatching rarely occur, and young hatched in November or earlier have been growing rapidly, so that the smaller size classes are not represented. Follicle growth is occurring gradually in adult females and some are many weeks ahead of others. Egg-laying becomes frequent in late March and young are becoming numerous by the end of April. Reproduction continues at a high level into early November, with females producing several successive clutches of eggs. Ovarian follicles develop slowly, since females recaptured over periods of weeks in March, April and May become more distended, seemingly from the same clutches of eggs. Young from eggs laid early in the breeding season would scarcely have time to reach mature size before the end of the breeding season; therefore, it may be inferred that one generation per year is the rule.

At Puerto Viejo, 71 km northwest of Turrialba, in the Caribbean lowlands, a series of 20 skinks was collected on 5 March 1965. These included hatchlings, older young of various sizes and five adult females, of which two had uterine eggs almost ready to be laid and the other three had large ovarian follicles. Obviously the halt in breeding in winter and spring indicated at Turrialba did not apply to this population living in a warmer and much wetter climate.

Greene (1969) examined 90 *S. cherriei* mostly from Costa Rica and found 16 gravid females, all from the months of March, May, June, July and August. Data concerning size of clutch (based on ovar-

ian follicles or uterine eggs) are available for 33 females including the 16 reported upon by Greene (1969) and 17 from Turrialba, Puerto Viejo and Beverly. Two each had one egg, 19 had two eggs and 12 had three eggs; $\bar{x}=2.33$. The size of the clutch tended to parallel size of the female.

DISCUSSION AND CONCLUSIONS

Every one of the many species and local populations studied had its own distinctive seasonal schedule and proved to be adapted in a somewhat different way from every other population to utilize the resources and avoid the rigors of specific environments. Although no two are just alike, there are several groups of species that are basically similar in their ecology.

The group that is probably the most different from all the others is that of the two giant iguanines, *Iguana iguana* and *Ctenosaura similis*. In addition to their large size these lizards have in common a largely herbivorous diet, relatively enormous clutches of eggs, with hatchlings that are remarkably small compared with the adults, a long period of growth, with sexual maturity postponed until late in the second year or even longer, and a breeding season extending over a small part of the year in the winter months. Typically oviposition occurs in the driest part of the year. As a result the incubating eggs receive maximum insolation. The young appear late in the dry season or early in the rainy season that follows it. The abundance of insects and of succulent vegetation in the early rainy season gives impetus to early growth. The timing of reproduction, though different from that of most other lizards in the same areas, is a logical one for areas having a pronounced dry season. However, *Iguana iguana* occurs also in regions that have consistently high precipitation and lack a marked dry season, and there is not much change in the timing of its reproduction. In rain forest and other situations of the Caribbean lowlands, where vegetation is dense, open areas of loose easily dug soil or sand for egg-laying may be of critical importance. Iguanas prefer riparian situations and often utilize open sandy banks or bars that may be submerged at flood stage. Timing of egg-laying so that eggs will be incubating during the driest part of the year is therefore of adaptive significance. In *Ctenosaura* the breeding season is more concentrated. The lizards live in relatively open situations, spend much of their time in burrows, and do much digging. Availability of nesting sites is probably less critical than in the iguana.

The largest group of species includes most of those that are characteristic of western Costa Rica in a climate characterized by a pronounced dry season—*Anolis cupreus, A. intermedius,* probably *A. biscutiger* and *A. sericeus, Cnemidophorus deppii, Ameiva undulata, Sceloporus variabilis* and probably *S. squamosus,* and *Gonatodes albogularis* in part of its range. All these are small or medium-sized species, insectivorous, oviparous and (except *Gonatodes*) heliothermic. They have a breeding season that extends through about half the year or somewhat more, including at least the months of May through October, the same individual producing eggs several or many times during this period. Then at the onset of the dry season or somewhat before it, reproduction declines to a low level or ceases entirely. For as much as half the year, November through May, there may be no reproduction. The population declines from its annual peak attained in late autumn. Meanwhile there is increase in average size. Some growth occurs in individuals of all size classes, and growth rates tend to be inversely proportional to the size of the individual. Consequently when the breeding season begins, the population consists of adults of various sizes, adolescents, and

immature lizards most of which are approaching adolescent size. As the breeding season progresses, there are steady increments to the breeding pool by newly maturing individuals until all or nearly all of the young from the previous season's crop have matured. Production reaches its annual peak at this stage. Meanwhile the first-laid eggs hatch and as hatchlings of this new crop begin to grow, they are replaced by successive increments of smaller ones. Eggs continue to hatch for several weeks after laying has ceased, and again the population builds up to an annual high point.

Two medium-sized, montane, viviparous insectivorous lizards, *Sceloporus malachiticus* and *Gerrhonotus monticola*, proved to have somewhat parallel trends in their annual schedules, and to differ from all other kinds. In both of them ovulations are concentrated in the June-August period, with births most frequent from early October to December. Reproductive activity thus is concentrated in the wettest and coolest part of the year. Young make most of their growth in the warmest and dryest part of the year and mature in time to produce litters of their own when they are about one year old. *S. malachiticus* conforms best to this schedule near the lower edge of its altitudinal range, as at Cartago in a relatively warm and dry climate. At higher elevation births are more evenly distributed through the year, and the lower temperatures retard gestation and growth, probably to the extent that an average generation extends over somewhat more than a year. In *G. monticola* also, there are some births throughout the year.

Two other viviparous lizards, *Mabuya mabouya* and *M. brachypoda*, differ from the above two species and each other in the timing of their reproduction. *M. mabouya* has births concentrated in March, indicating breeding activity some weeks earlier, perhaps in December, with gestation in the driest part of the year when sunshine for basking is most frequently available. Advent of the young is timed for a period of heavy precipitation. *M. brachypoda*, living in the drier climate of the Pacific versant, has its main breeding season delayed some four months later than that of *M. mabouya*. This results in a gestation that is timed for the early weeks of the rainy season, but in an area where there is generally sunshine for a part of each day permitting regular basking. Births are concentrated near the middle of the rainy season.

Basiliscus basiliscus has an annual schedule different from that of any other species and seemingly its populations differ notably among themselves at localities that are similar in habitat and not far apart. At Finca Taboga the dominant groups of young were from eggs probably laid in February, late March-April, July and August, with much less egg-laying at other times of year. At La Irma large crops of young resulted from egg-laying from October to November-December, and February. At Río Naranjo there were large broods from early November and December laying. On the Meseta Central there were broods from eggs laid in early December both at Turrúcares and Ojo de Agua.

A group of small to medium-sized, insectivorous species that are much alike in their annual cycles all occur in the Caribbean versant in climates of high rainfall and no marked dry season. They include *Basiliscus vittatus*, perhaps *B. plumifrons*, *Anolis limifrons*, *A. humilis*, *Scincella cherriei*, *Ameiva festiva*, *A. quadrilineata* and *Lepidoblepharis xanthostigma*. In all there is probably some breeding throughout the year. In *A. humilis* at Beverly there was relatively little egg production in January-March as compared with the rest of the year. In *A. limifrons* at Beverly

the same slowing in winter and spring was evident and it extended through April, with peak production in August and September. In *Basiliscus vittatus* at Portéte there was a three-month pause in reproduction that extended over much of November and to early February. In *Scincella cherriei* at Turrialba reproduction virtually stopped during a similar period—December to March. In these species reduced reproduction corresponds with the colder part of the year. However, the seasonal temperature change is slight, and each of the species lives and reproduces in cooler climates than those at the study areas. Seasonal variation in rainfall is much greater. February and March are usually by far the driest months of the year, with January and April also below average. Rainfall seems the most obvious variable that might affect level of reproductive activity. However, in *S. cherriei* and especially in *B. vittatus* the pause in breeding begins at a time when rainfall is still extremely high in November and December, hence it is not a direct result of reduced precipitation.

In a climate having little seasonal change in precipitation or temperature, it might be expected that population structure and level of reproductive activity would change but little in the course of an annual cycle. The species that was found most stable in this respect was *Anolis tropidolepis* at Hacienda El Prado on the Continental Divide in a cool moist climate. Although the amount of precipitation is much less in February, March and April than at other times of year, fog and rain are frequent at all seasons so moisture is never in short supply. Females of *A. tropidolepis* seem to produce eggs uninterruptedly throughout the year. Hatchlings and young of all sizes are always present and their ratios do not show any consistent trend; it is doubtful whether there is any significant seasonal change in the level of reproductive activity. *A. lionotus* also seems to reproduce throughout the year with no seasonal change at San Miguel de Sarapiquí. However, samples are relatively small for this species and are not ideally distributed through the year. Until more is known about the method of obtaining food and the sites of egg-laying, little can be said about the effect of precipitation on *A. lionotus*. In its streamside habitat moisture is never in short supply. Precipitation raises the stream level submerging rocks and logs that are used for perches at other times and reducing the open area at the edge of the water, in which most activity occurs. It reduces water temperature but increases the volume and rate of flow. It increases the quantity of floating arthropods, and probably decreases the availability of subaquatic arthropods, which are more dispersed and more deeply submerged.

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EXPLANATION OF PLATES

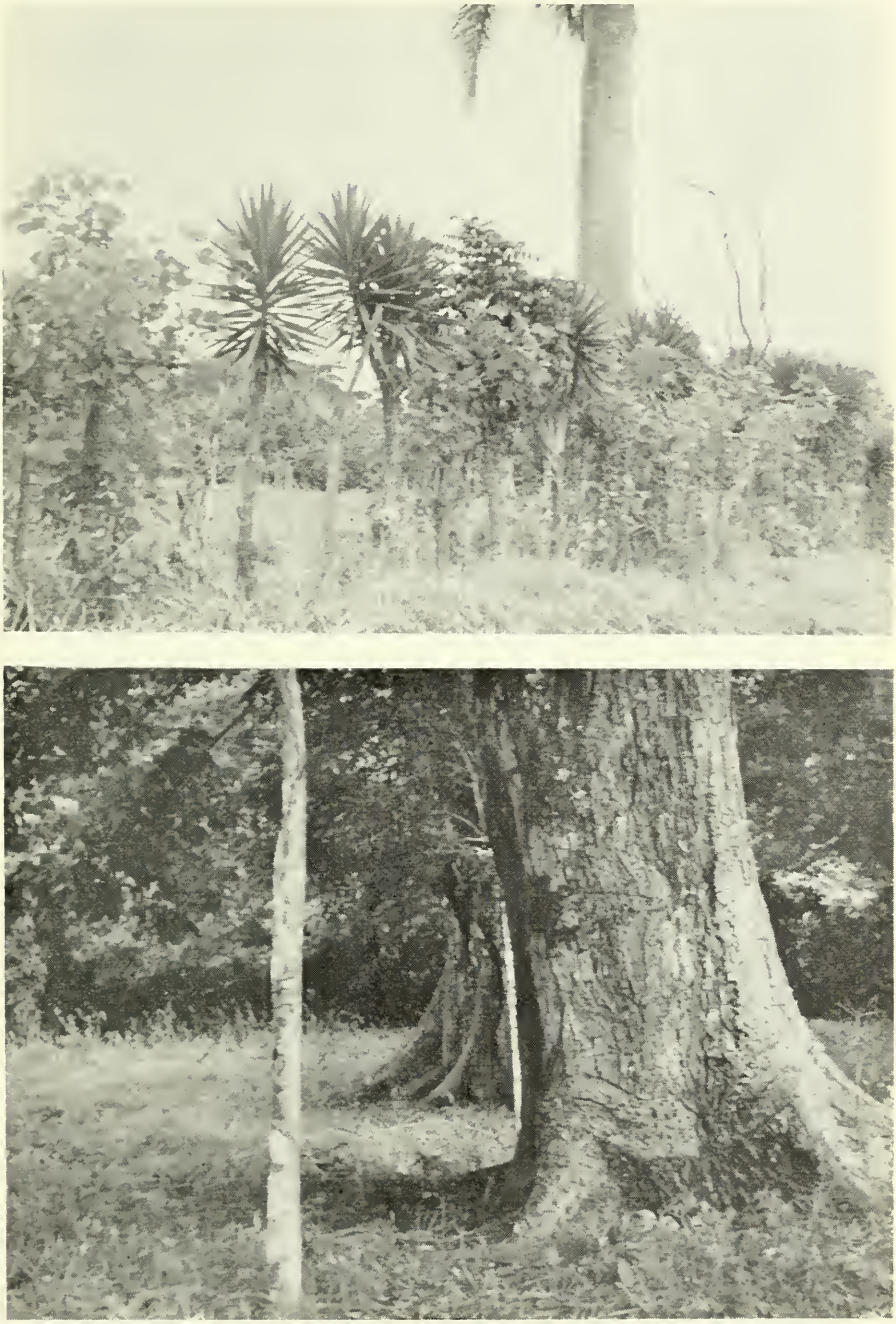

Plate I. **Upper,** fence in San José utilizing yuccas and other trees as posts; **lower,** study area no. 2 at Playas del Coco; many *Sceloporus variabilis* lived on spiny trunks of the two large trees *(Bombacopsis quinata).*

PLATE II. **Upper,** beach wrack at Boca de Barranca; **middle,** upper beach at Boca de Barranca; **lower,** log jam in the dry season at Río Congo, La Irma.

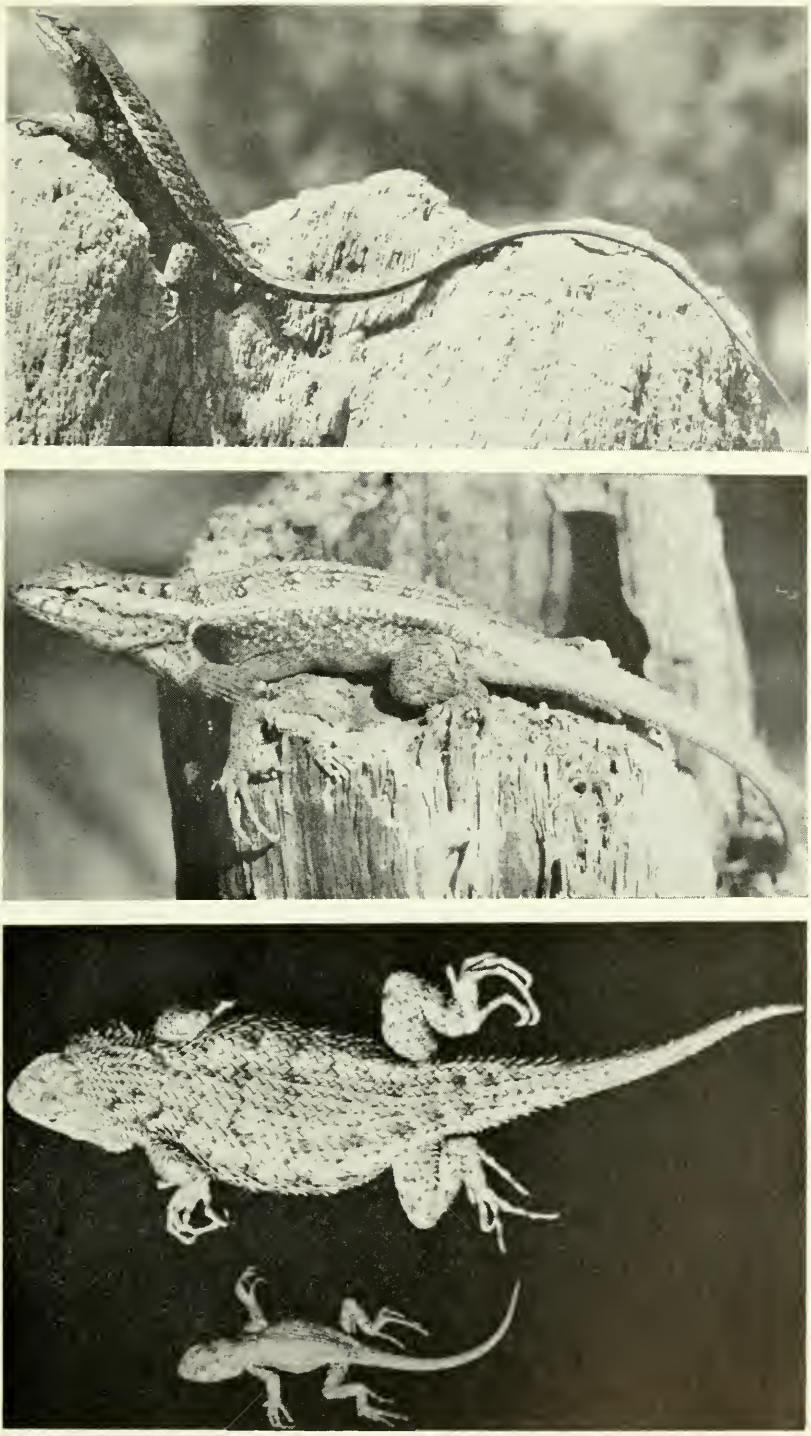

Plate III. **Upper,** *Sceloporus squamosus,* adult male, Playas del Coco; **middle,** *Sceloporus variabilis,* adult male, Playas del Coco; **lower,** *Scelophorus malachiticus,* adult female with one of her five newborn young, Hacienda El Prado.

PLATE IV. **Upper,** *Ameiva undulata,* adult male, Sardinal; **upper middle,** *Cnemidophorus deppii,* adult male, Boca de Barranca; **lower middle,** *Anolis cupreus,* adult male, San José; **lower,** *Anolis sericeus,* adult male, La Irma; **lower left,** *Gonatodes albogularis,* adult male, Boca de Barranca.

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A COMPARISON OF VARIOUS TECHNIQUES OF MULTIPLE FACTOR ANALYSIS APPLIED TO BIOSYSTEMATIC DATA

By
DAVID R. FISHER

Vol. 50, No. 3, pp. 127-162 November 13, 1973

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A Comparison of Various Techniques of Multiple Factor Analysis Applied to Biosystematic Data

David R. Fisher

A Comparison of Various Techniques of Multiple Factor Analysis Applied to Biosystematic Data[1, 2]

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Department of Zoology
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ABSTRACT

This paper is an investigation into the similarities and differences between the nonstatistical factor analyses, centroid (CFA), and principal (PFA); and the statistical factor analyses, image covariance (ICFA), alpha (AFA) and canonical or maximum likelihood (MLFA). The nonstatistical factor analyses scale the correlation matrix by placing the communalities in the diagonal, while the statistical factor analyses scale the entire matrix. The statistical factor analyses assume that either the observations, variables, or both are a population, rather than samples from a population. A statistical factor analysis which assumes that both are samples has not yet been developed.

Five data sets were chosen to study the different factor analytic techniques. The data sets were: (1) a homogeneous sample of pigeon skeletal measurements; (2) morphometric measurements from three species of fishes; (3) morphometric measurements from a taxonomic study on a heterogeneous group of lizard genera; (4) a more homogeneous subset of the previous data set; and (5) a set of biogeographic data. The data were analyzed by the NT-SYS programs of Rohlf, Kishpaugh and Bartcher on the GE-635 Computer at the University of Kansas.

The five data sets were analyzed by each of the five techniques of factor analysis. Each unrotated factor solution was rotated to an oblique solution by MTAM (a mass modification of Thurstone's analytical method) and some were also rotated to an orthogonal solution by Varimax. From the pigeon and fish data sets, three different numbers of factors were extracted. From the remaining data sets, only one number of factors was extracted.

The results show that OTUs sampled from singles or homogeneous populations gave multiple factors which have reasonable interpretations in terms of the biology of the organisms. This occurred in the pigeon and fish data sets. In samples including several species, as shown by the lizard data, the factors made little biological sense. Results from the fish distribution data were readily interpretable and led to hypotheses about the distributions concerned.

A summary of the congruences of the factors from different techniques on each of the five data sets showed that the nonstatistical techniques, PFA and CFA, consistently gave better results. Some of the statistical techniques gave good results, but none were as consistently good as these two methods. A good solution was defined in terms of simple structure; i.e., no factors with low correlations with most of the variables and few variables having high loadings on several factors. Other criteria were that a good solution included those factors which were most consistently found by all techniques and had reasonable biological interpretations.

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[1] This paper was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Kansas.

[2] The study was supported in part by grant GM-11935 from the National Institute of General Medical Sciences to Dr. Robert R. Sokal.

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A comparison of rotations showed that MTAM was extremely sensitive to the extraction of too many or too few factors. In addition, it sometimes gave different results, depending upon the factoring technique, for factors associated with only a few variables. Varimax was less sensitive to extraction of the "wrong" number of factors and often gave the same results independent of the factoring technique.

The study concluded that the correct number of factors can be found by extracting more than one set of factors, using both an oblique and an orthogonal rotation, and selecting the final solution from this set.

For smaller data sets, any factoring technique took very little computer time. For the larger data sets, only PFA and CFA were feasible. For the very largest data sets, only CFA could be computed in a reasonable length of time.

INTRODUCTION

Variables in systematics and ecology, as in psychology, are often not amenable to experimental manipulation. For example, organisms and ecological systems are a product of evolutionary variables which have acted in an unknown manner. Often, the events under investigation have occurred and therefore cannot be observed. However, it may be possible to make observations on variables as they exist in the present state in nature and to summarize these variables in a form which might be interpretable in terms of possible evolutionary history or ecological forces. Multiple factor analysis is a multivariate statistical technique compatible with the above stated purposes (Thurstone, 1947; Cattell, 1952, 1965a, 1965b; Fruchter, 1954; Sokal and Sneath, 1963; Lawley and Maxwell, 1963; Seal, 1964; Harman, 1967; and Morrison, 1967).

Multiple factor analysis is thus utilized when variables related to a phenomenon are observed, but not *a priori* understood in terms of underlying relationships, and cannot be experimentally manipulated. If a considerable amount of redundancy exists among the variables, i.e., they are correlated, they can be summarized by fewer hypothetical variables or common factors. If, in addition to this parsimonious description, the factors shed light on possible causal relationships among variables, one will have obtained an even more elegant description of the system. In systematics and ecology, one might expect that morphological and ecological data collected from a group of organisms might reflect a number of patterns related to their evolutionary or ecological history. In the voluminous biodistributional data available to the biogeographer, fewer or simpler trends or groups might be interpreted in terms of the distributional history of the organisms.

This paper compares and evaluates different techniques of multiple factor analysis. The computations in factor analysis are laborious and in the past workers restricted themselves to the simpler techniques, such as centroid and principal factor analyses. Yet, psychometricians (who were pioneers in the development of this field) have recently developed more complex techniques, which they believe to be more powerful. These include canonical, alpha, and image covariance factor analyses. The newer techniques involve more computation, yet it has not been clear whether they give significantly improved factor solutions than the simpler approaches. In this paper I shall investigate the similarities and differences among solutions by these various techniques to determine when they might best be utilized over the less rigorous methods.

Notation for matrices in factor analysis varies from author to author. For example, the matrix of factor loadings is

A in Harman (1967), **F** in Thurstone (1947), and **F** in Jones (unpubl.). Since none of these authors discuss all the factor analyses considered here, it is not possible to be completely consistent with all of them. For this reason, the most important matrices described in this paper will be defined at this point. They are based on p variables ($i=1, 2, \ldots p$), n observations ($l=1, 2, \ldots n$), and k factors ($J=1, 2, \ldots k$). The meanings of the various matrices and vectors will be defined in the appropriate places in subsequent sections.

Matrix	*Elements of Matrix*	*Description of Matrix*
E		Eigenvectors, p rows by k columns
F	f_{ij}	Factor loadings, p rows by k columns
$\mathbf{f}_j$		jth vector of factor loadings, p rows by 1 column
H=I–U	h_i	Communalities, diagonal matrix, p rows by p columns
I		Identity matrix, diagonal of ones
Λ	λ_j	Eigenvalues, diagonal matrix, k rows by k columns
M		Scaled correlations, p rows by p columns
P	p_{ij}	Factor scores, n rows by k columns
R	r_{ij}	Sample correlations, p rows by p columns
R*		Correlations with communalities in the diagonal, p rows by p columns
U=I–H	u_i	Uniquenesses, diagonal matrix, p rows by p columns
V	v_{ij}	Rotated factor loadings, p rows by k columns
X	x_{il}	Observations, p rows by n columns
X*	x^*_{il}	Standardized observations, p rows by n columns

Centroid Factor Analysis (CFA) is reviewed by Thurstone (1947) and Harman (1967). It has been primarily used as an approximation to calculating the Principal Factor Solution (see the next section). Recently, with the general availability of electronic computers, principal factor analysis has replaced CFA. However, since CFA requires substantially less computation than other methods, it is still useful for handling large data sets (e.g., $p>100$). The method is used in place of calculating eigenvectors. Normally, the correlation matrix is not scaled: $\mathbf{M}=\mathbf{R}^*$ and $\mathbf{F}=\mathbf{E}$. The factor loadings are calculated by $\mathbf{f}^t_1 = (\mathbf{1}\cdot\mathbf{R})[\sqrt{\mathbf{1}\cdot\mathbf{R}\cdot\mathbf{1}^t}]^{-1}$, where $\mathbf{f}_1$ is the first centroid factor and **1** is a 1 by p vector of ones. **R** is then reduced by $\mathbf{R}'$, the reproduced correlations: new $\mathbf{M}=\mathbf{R}-\mathbf{R}'$, where $\mathbf{R}'=\mathbf{f}_1\cdot\mathbf{f}^t_1$. Next, appropriate variables are reflected so the centroid of the residual matrix is as positive as is possible, and the next factor is extracted and so on, up to k factors. Finally, the Communalities are re-estimated and the process is repeated.

Principal Factor Analysis (PFA), like CFA, starts with the matrix $\mathbf{R}^*$, the correlation matrix with communalities in the diagonal. Then eigenvectors and eigenvalues are calculated. Since $\mathbf{M}=\mathbf{R}^*$, $\mathbf{F}=\mathbf{E}$. PFA is discussed by Harman (1967). An approximation to PFA, common previous to the general availability of computers, was to estimate the communalities and accept the factors calculated without any iterations as a fairly reliable estimate of the iterated factors. This approximation procedure should no longer be used.

CFA and PFA can be thought of as nonstatistical analyses. The unrotated factors are calculated by considering the variables as vectors plotted in the sample space according to their correlations (see Gower, 1967). Each variable vector i is of length h_i, owing to the scaling procedure of these techniques. The factors are then computed as the centroids or principal axes of $\mathbf{R}^*$.

Image Covariance Factor Analysis (ICFA) is reviewed by Guttman (1953, 1956), Kaiser (1958b) and Horst (1965). It was developed as a factoring technique

which would have a statistical basis, while avoiding the problem of an iterative estimate of the communalities. This was done by assuming that both the variables and observations constitute a statistical population and that the common variation is the variation in each variable which is explained by the presence of the other variables. The communalities are then the squared multiple correlation coefficients. These are placed in the diagonal while the off-diagonals are adjusted so that they reflect only common variation. The factors chosen can be those for which the eigenvalues are greater than 1.0. One difficulty in calculating the **M** matrix in ICFA is that $\mathbf{R}^{-1}$ may not be defined (this is the case if there are fewer observations than variables). If $\mathbf{R}^{-1}$ is not defined, a generalized inverse -**G**- must be used for the estimates of the multiple correlations:

True multiple correlations, $\overline{\mathbf{R}} = \mathbf{I} - (\text{diag}\,\mathbf{R}^{-1})^{-1}$.

Estimated multiple correlations, $\overline{\mathbf{R}} = \mathbf{I} - (\text{diag}\,\mathbf{G})^{-1}$, where $\mathbf{G} = \mathbf{E} \cdot \Lambda^{-1} \cdot \mathbf{E}^t$, and **E** is a matrix of eigenvectors with eigenvalues greater than 0., and Λ is the diagonal matrix of associated eigenvalues. The correlation matrix, **R**, is scaled as follows:

$\mathbf{M} = \mathbf{R} + \mathbf{U}^2 \cdot \mathbf{R}^{-1} \cdot \mathbf{U}^2 - 2\mathbf{U}^2$ and $\mathbf{F} = \mathbf{E}$.

Canonical Factor Analysis (MLFA). Lawley (1940) proposed a statistical factor analysis based upon maximum likelihood considerations, maximum likelihood factor analysis. The advantage of such an approach is that it is related to distribution theory and, therefore, statistical tests can be performed. As originally proposed, the solution often did not converge and was scaled in an arbitrary manner. For these reasons, many authors, Jones (unpubl.), Morrison (1967), and Lawley and Maxwell (1963), prefer an alternative solution, canonical factor analysis, proposed by Rao (1955). In this case, the solution implies the following scaling procedure:

$\mathbf{M} = \mathbf{U}^{-1} \cdot \mathbf{R}^* \cdot \mathbf{U}^{-1}$ and $\mathbf{F} = \mathbf{U} \cdot \mathbf{E}$.

The technique is scale free; i.e., scale changes in **X** do not affect **F**. The number of factors is decided by sequential testing. After extracting a new factor, the matrix of roots, or eigenvalues, is used to test for completeness of factor extraction and if successful, the process is stopped. Otherwise, an additional factor is extracted with the new communalities solved for iteratively, and a new test is calculated, and so on.

The metric of MLFA is in terms of the uniqueness, giving variables with a low uniqueness more weight. In most biological data only a few variables have high uniqueness, but these have already been given a low weight by the calculation of $\mathbf{R}^*$. Another aspect of MLFA is the assumption that the variables are a population and the observations are a sample. Since biological variables are almost always a sample (except possibly in geographic distribution, where all known species distributions from a locality could be included), this assumption is not realistic.

Alpha Factor Analysis (AFA) was proposed by Kaiser and Caffrey (1965) as an alternative to canonical, or maximum likelihood, factor analysis. Unlike CFA and PFA, and like MLFA it is scale free—the same factors result no matter what the scale of the original data matrix was. This means that standardization of **X** is unnecessary (except to help prevent rounding errors in computing **R**). The scaling procedure used by AFA was derived by maximizing the correlation between the calculated common factors and their universe or "true" common factors. Kaiser and Caffrey defined this as maximum generalizability. A further assumption of the technique is that the variables are a sample and the observations are a population. The scaling of **R** is in terms of the inverse of the communalities. The method of scaling is: $\mathbf{M} = \mathbf{H}^{-1} \cdot \mathbf{R}^* \cdot \mathbf{H}^{-1}$ and $\mathbf{F} = \mathbf{H} \cdot \mathbf{E}$.

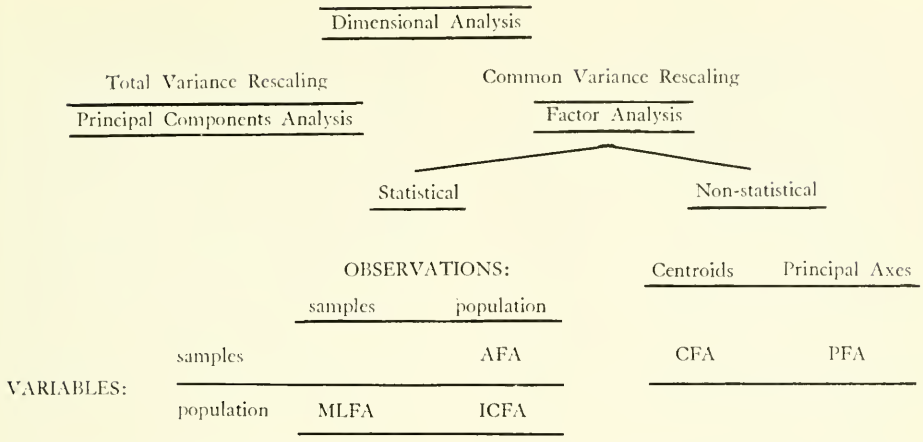

Fig. 1. A comparison of the five techniques of factor analysis and of principal components analysis. Modified from Jones (unpubl.).

The advantages of AFA, according to Kaiser and Caffrey, are that the scaling is in terms of the common parts (i.e., the variables of major interest), **M** is a correlation matrix (**M** in MLFA has no such interpretation), and the number of factors chosen is usually that set for which the corresponding eigenvalues are greater than 1.0. The number of eigenvalues greater than 1.0 is the same in both **R** and **M**. Kaiser's scaling metric may or may not be an advantage, since it gives low weights to the variables of major interest. This is because the variables with high communalities are those which should appear in the factors, while those with low communalities should not. One might expect that the technique would have problems with data which contain many variables with low communalities. This did, in fact, occur and will be discussed below. Another difficulty is that the method of determination of number of factors recommended by Kaiser did not prove to be practical in data sets studied here. Usually too many or too few factors resulted. The assumption about the variables being a sample and the OTUs being a population is no more realistic for most biological data than the opposite one of MLFA. This is especially true in small samples where clearly an insufficient number of OTUs have been sampled to allow an accurate estimate of the variance of each variable in the population. However, in larger samples violation of this assumption would probably not be too serious.

A comparison of the above techniques is shown in Figure 1. AFA, MLFA and ICFA are characterized as statistical factor analyses due to their derivations from statistical models, while CFA and PFA are characterized as non-statistical due to their derivations from geometric models.

Factor Analysis in Biology. Until recently, almost all factor analytic studies in biology used CFA or PFA. Of the papers discussed below, either CFA or an unstated method of factor analysis was used (probably principal components analysis or PFA without iteration for $\mathbf{H}^2$ by using an initial estimate of some sort). Smith and Fisher (1970) used PFA for comparison with the results from CFA. Since these studies used CFA or PFA, the effects of scale were removed by computing the factors from the correlation matrix.

All the studies discussed (except for Morishima and Oka, 1959) rotated to

simple structure. Stroud (1953) used Thurstone's method (Thurstone, 1947); Wallace and Bader (1967) used Varimax (Kaiser, 1958a); Gould (1967), Gould and Garwood (1969) and Gould (1969) used an unstated method; while the remaining studies used MTAM (Sokal, 1958). Sokal, Daly and Rohlf (1961) and Sokal and Daly (1961) compared the results from MTAM (they were essentially orthogonal) to results from Varimax, and found them similar. It should be noted that principal components analysis is not factor analysis, and workers using rotation of a principal components solution are not solving for a correctly accepted model; hence, their resolution and interpretation may be subject to question. Examples include the Gould papers mentioned above.

All the factor analytic methods described are R-type analyses (Cattell, 1952); that is, factors are extracted from the correlation of variables matrix. It is also possible to start with a matrix of correlation of samples or OTUs and extract factors from this matrix. This is a Q-type study. The disadvantage of this method is that the distributions of the samples are probably discontinuous, or at least not normal. The approach is reasonable if special care is taken to see that the distributions of the samples are somewhat normal. If they are not, the correlations do not estimate parametric correlation coefficients and the factor extraction process might be adversely affected. A better approach would be to calculate a matrix of factor scores, (see Harman, 1967, for a discussion of factor scores).

Problems Previously Analyzed. One of the biological problems which has been analyzed by factor analysis is that of finding patterns of variation in morphometric data. Sokal (1962) analyzed intragall correlation matrices of the aphid *Pemphigus populi-transversus* as part of a geographic variation study of this aphid. Wallace and Bader (1967) factor-analyzed 27 mouse bone measurements. They extracted five factors. This study was done to demonstrate the interrelationship of bone characters. One would hope that future studies would be used to answer a specific biological question, rather than to simply summarize data. Gould (1967), Gould and Garwood (1969) and Gould (1969) studied morphometric data analyzing patterns of variation in fossil animals. Gould relates the characters loading on a particular factor with levels of "integration" and feels that these are related to evolutionary patterns in characters. He did not, however, discover which characters had unique patterns, since he did not iterate for the communalities and, therefore, did not discover which characters had a high uniqueness. In the study of evolutionary patterns, groups of covarying characters are certainly of interest, but so are characters with high uniqueness. Sokal and Rohlf (1970) factor analyzed bee characters measured by a taxonomist and two "Intelligent Ignoramuses."

There have been several taxonomic studies using factor analysis. Some of these have, in addition, stressed the morphometric aspect of their data. The Gould studies described above might also be considered taxonomic, since some of the data were from different taxonomic groups. Stroud (1953) in a morphometric and taxonomic study compared factors from 14 measurements on two life stages of the termite species *Kalotermes*. Forty-eight examplars of the soldier and imago stages were measured yielding five soldier factors and six imago factors. One factor was found to be congruent between the two groups. The evolutionary significance of the patterns, or factors, was discussed. Rohlf (1962) compared factor analyses on adult and larval characters of the mosquito genus *Aedes* finding some factors similar and some factors unique to the separate stages.

Factor analytic studies which have been purely taxonomic include part of Stroud (1953). He projected standardized data onto his first factor to cluster the OTUs. On this basis, a new taxon (to be considered a subgenus of *Kalotermes*) was proposed. The remaining studies used Q-type factor analysis. Morishima and Oka (1959) employed plots of each pair of unrotated factors of OTUs to classify 16 species of the genus of rice *Oryza*. The studies of Rohlf (1962), Rohlf and Sokal (1962) and Rohlf (1967) are other examples of Q-type factor analyses. The factors become abstract "types"; i.e., each factor is associated with a group of OTUs for which it separates an abstract representation of basic morphological form. Probably a better approach in most of these studies would have been a factor analysis on the characters; i.e., an R-type analysis and projection of the OTUs within an A-space (attribute space—Williams and Dale, 1965). Even using this approach, there is no way to accurately display the relationships between the OTUs for classificatory purposes, unless of course only three or fewer factors are sufficient. If, however, the OTUs form "good" clusters, then each group will be associated with a single factor (as was found by Rohlf and Sokal, 1962). Even so, if the purpose of the study is taxonomic, the investigator should be interested in displaying the relationships between the OTUs and, for this purpose, the current three-dimensional approach described by Rohlf (1967, 1968) is superior.

Factor analytic studies of geographic variation include Sokal (1962), Sokal and Rinkel (1963) and Sokal and Thomas (1965). They compared intergall and interlocality correlation matrices of the aphid *Pemphigus populi-transversus* from several localities in North America. The factors relating the different levels of variation were different and reflected different types of variation. For each factor the areas, where the projections onto them were uniform, were very roughly outlined on maps of the eastern United States. Another significant aspect of these studies is that this was the first attempt to reduce the massive amounts of data available on a number of variables in a study of geographic variation in such a way that patterns of variation in populations could be displayed in terms of a few factors.

Fisher (1968) and Smith and Fisher (1970) used factor analysis to summarize patterns of geographic distribution. Fisher's (1968) was primarily a methodological investigation. In the second paper, 130 variables, consisting of the distributions of all the fish of Kansas and 28 selected environmental variables, were scored in 96 drainage units. Eight factors were extracted. Locality maps for the factor scores were drawn using trend surface analysis and presented as faunal patterns associated with environmental and historical variables. The faunal patterns were not mutually exclusive.

Factor analysis has also been used in an attempt to discover cause and effect relationships in biological data. Sokal, Daly and Rohlf (1961) and Sokal and Daly (1961), in an attempt to see if factor analysis was a valid approach to study cause and effect phenomena, utilized factor analysis in a study of insect behavior. Nineteen behavioral and physiological variables, e.g., heart rate, activity rate, etc., were measured on various insects. Six putative "causal" environmental variables such as temperature and humidity were also measured. Six factors were extracted from the complete matrix. They were essentially uncorrelated. A test of factor invariance was made by dividing the data into two sets of biological and nonbiological variables. Factors extracted from these two sets were comparable to those found in the complete set. The investigators also found that MTAM gave "poor" results

(difficult to interpret) when "too few" factors were extracted. Wenner, Wells, and Rohlf (1967) investigated the bee dance hypothesis of von Frisch. The data consisted of both environmental variables and behavioral variables. They found that the bee dance hypothesis was not corroborated on the basis of their results. The variables representing various parameters of the dance were not found to be associated with the same factors as variables relating to the food source. The study included other multivariate analyses, which supported the factor analytic results.

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The University of Kansas offered generous support in computing funds.

MATERIALS AND METHODS

The following five data sets were employed in this study.

The Pigeon Data Set, Figure 2, from Olson and Miller (1958), describe five random samples of 20 individuals each of domestic pigeons, *Columba livia.* Both males and females were included. The samples were collected near the campus of the University of Chicago. These wata were selected as an example of a data set with a small number of variables and sampled from a homogeneous population. They consisted of 26 bone and skull measurements. The data had been factor analyzed previously by Rohlf (unpubl.) and had been found to give clear cut, easily interpretable factors.

The Fish Data Set, Smith (unpubl.), represent a data set with a small number of variables, in which the OTUs were more heterogeneous than in the pigeon data. The 87 OTUs were individual specimens in a local sample of fish, consisting of 3 species *Rhinichthys osculus* (Girard), 23 individuals; *R. cataractae* (Valenciennes), 27 individuals; and *Richardsonius balteatus* (Richardson), 34 individuals. Three specimens collected were thought to be interspecific hybrids. A principal components analysis showed that the three populations are phenetically distinct, forming ellipsoids in the three-dimensional space of the first three principal axes. The axes for the ellipsoids for each of the populations are parallel. This means that although the populations are distinct, they vary in a similar fashion for the characters measured. Thirty-nine characters were measured, including meristic and morphometric features, in addition to color characters, specifically designed to differentiate these three populations.

The Complete Lizard Data Set, Fisher (1973), consists of a heterogeneous group of species of 90 iguanid lizards from the American Southwest. The 90 OTUs comprised five specimens (in a few cases, four) for each of 19 species. They included seven similar species, recognized in two genera, belonging to a group called sceloporines (but without formal taxonomic status); nine moderately different species, assigned to six genera, but still forming a phenetic group with the sceloporines; and three species in three separate genera, one of which represents a second group called iguanines, and two of which are distinct—not part of any subgroup of iguanines. The study (by principal components analysis) demonstrated that the sceloporines formed a phenetically distinct group separated by gaps from the two distinct genera and from the single iguanine species. The 130 characters consisted of lengths, widths, scale counts, scale sizes, and a few presence-absence characters. Only a few characters, describing foot scales and lengths and head scales, were in the dimensions separating the iguanine species from the sceloporines.

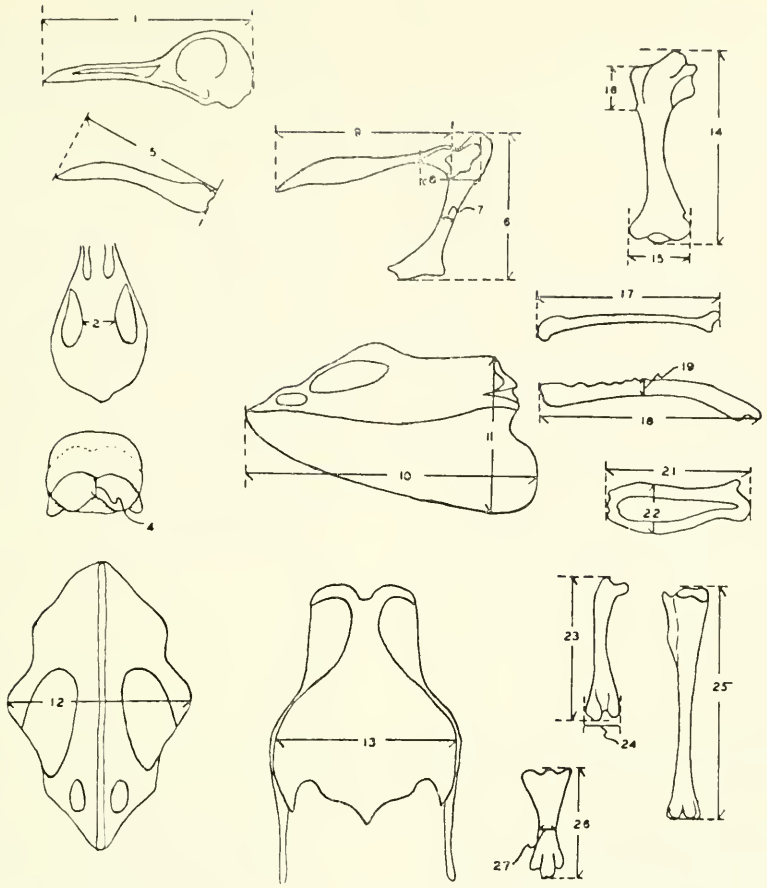

Fig. 2. The 26 variables for the pigeon data showing how the bones were measured (from Olson and Miller, 1958, with permission of the publisher).

Description of Characters

1, Length of skull tip of beak (bone) to middle of crest on occiput, giving maximum; **2,** Interorbital width, minimum normal to mid-line of skull; **3,** Anterior end of narial opening to tip of bony beak; **4,** Height of occiput, from top of foramen magnum to mid-point of crest at top of occiput; **5,** Length of lower jaw, maximum; **6,** Length of coracci along anterior border; **7,** Minimum width of coracoid in outer aspect; **8,** Maximum width of glenoid fossa; **9,** Length of scapula, maximum; **10,** Length of keel on sternum maximum; **11,** Depth of keel, anterior at level of anterior margin of pillar; **12,** Width of sternum, maximum; **13,** Maximum width of dorsum of scarum; **14,** Maximum length of humerus; **15,** Distal width of humerus, dorsal orientation; **16,** Length of major trochanter of humerus, tip of proximal end to end of muscle scar, distally; **17,** Maximum length of radius; **18,** Maximum length of ulna; **19,** Width of ulna, dorsal aspect, between feather scars nearest middle of bone; **21,** Length of largest metacarpal; **22,** Maximum depth (width) of metacarpals 3 and 4, oriented with condyle level; **23,** Length of femur, maximum; **24,** Distal width of femur, condyle maximum; **25,** Maximum length of tibia-fibula; **26,** Maximum length of mid-metatarsal; **27,** Minimum width of metatarsal complex.

The entire data set of this study is here called "the complete data set."

The Reduced Lizard Data Set is restricted to the seven similar scleoporine species mentioned above. It consisted of 33 OTUs. The same 130 characters were employed. This reduced data set was included so that the techniques of factor analysis could be compared for very heterogeneous data in groups separated by large gaps (the complete lizard data set) and less heterogeneous data consisting of

fairly similar groups, i.e., not separated by gaps (the reduced lizard data set).

The Fish Distribution Data Set, Smith and Fisher (1970), was selected as an example of a distributional study. They represent the presence or absence of 105 species of fishes and 28 environmental variables recorded for 96 drainage units in Kansas. Smith and Fisher (1970) calculated a CFA solution with eight factors which was rotated to simple structure by MTAM. The factors were identified as: large river fishes distributed independently of environmental variables; widespread prairie and plains stream fishes whose pattern of distribution was highly correlated with environmental variables; cold water relicts, a subset of the distributions found by the previous factor, but having low correlations with environmental variables; warm-water stream fiishes, whose distributions were highly correlated with runoff and length of growing season; fishes historically centered in the Osage River and distributed independently of environmental variables; fishes historically centered in the Neosho River and highly correlated with environmental variables, especially permanent water; fishes historically centered in the Spring River and part of the Ozark plateau fauna; and a factor of mostly environmental variables, which appear to predict fish diversity in Kansas. Correspondence between the CFA solution and a solution using PFA was found to be good. The PFA solution combined a new arrangement of the factor of southern warm water fish distributions not as highly correlated with temperature. The noncongruent factors from the two techniques were associated with few variables and present restatements of variation already present in the seven congruent factors. The data were included here for comparison of the PFA and CFA solutions (which were considered very good) with the statistical factor analyses.

Methods of Computation. The computations were carried out on the GE-635 computer at The University of Kansas Computation Center using the NT-SYS programs developed by Rohlf, Kishpaugh and Bartcher. The computational procedure is shown in Figure 3. In all five factor analyses the initial communalities were the squared multiple correlation coefficients. PFA and CFA were available as precoded subroutines in NT-SYS, which estimated the communalities iteratively and calculated the unrotated factor matrix. For ICFA, the **R** matrix was scaled to the **M** matrix (see Fig. 3) by the matrix algebra subsystem of NT-SYS. The factors were extracted from the **M** matrix by the principal axes subprogram. AFA and MLFA were calculated in a more complex fashion. The **R** matrix was scaled to **M** (see Fig. 3) by the algebra routine, the factors extracted by the principal axes routine, **F** calculated from **E** by the algebra routine, the communalities re-estimated from the factors by the algebra routine, and finally the **M** matrix was recalculated to start the next iteration. Varimax (Kaiser, 1958a) and MTAM (Sokal, 1958) were both available as NT-SYS routines.

Solutions for three different numbers of factors for all techniques were calculated for the pigeon and fish data sets. For the other three data sets, limitations on computing time forced the selection of only one solution per data set per technique. These nine unrotated solutions are represented by the nine columns of Table 1. Within each column of Table 1, a comparison was made between either the orthogonal solutions (the elements of Table 1 with a V) or the oblique ones (the elements of Table 1 with a M). The comparisons were made using a method given in Harman (1967) following Wrigley and Neuhaus (1955). The formula, expressed in matrix notation, is as follows:

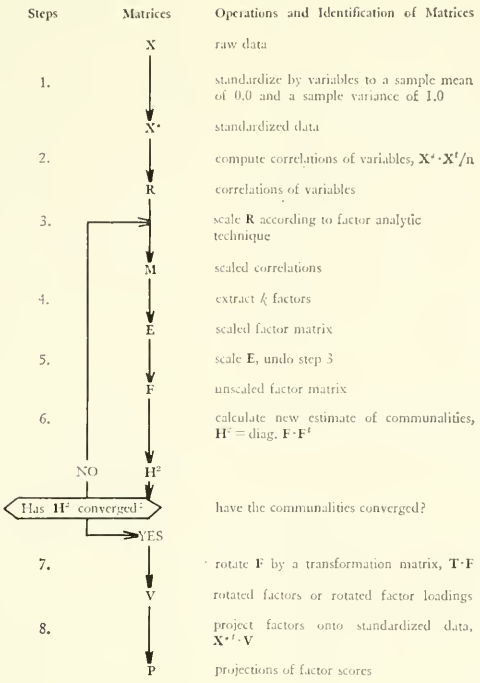

FIG. 3. The computational steps of factor analysis, discussed in the Materials and Methods section. Column 2 is each matrix in the computational steps. Columns 1 and 3 are the number and description of each operation.

$$\mathbf{C} = \sqrt{(\text{diag } \mathbf{F}^t_1 \cdot \mathbf{F}_1)^{-1}} \cdot (\mathbf{F}^t_1 \cdot \mathbf{F}_2) \cdot \sqrt{(\text{diag } \mathbf{F}^t_2 \cdot \mathbf{F}_2)^{-1}},$$

where $\mathbf{F}_1$ is one factor matrix, $\mathbf{F}_2$ is the other and $\mathbf{C}$ is the matrix of congruences. The elements of $\mathbf{C}$ vary between +1.0 and −1.0. Each row of $\mathbf{C}$ refers to each one of the factors of the first solution, and each column refers to each one of the factors of the second solution. Perfect congruence would be 1.0 once in each row and column of $\mathbf{C}$ (not necessarily in the diagonal, but the rows and columns could always be rearranged so that the 1.0's are in the diagonal).

RESULTS

The results consist of 65 rotated matrices, calculated from 45 unrotated factor matrices. This is shown in Table 1; each data set for a different number of factors (nine columns) and each technique (five rows), giving 9×5 or 45 unrotated solutions. All of the 45 unrotated solutions were rotated by MTAM (the columns of Table 1 with a M). Several were rotated by Varimax (the columns of Table 1 with a V). The CFA factors and the two extra solutions for the pigeon and fish data were not rotated by Varimax, to reduce the number of comparisons.

Six of the above rotated factor matrices are shown in Tables 12 to 17. The rest are not included. The factor loadings are coded with the same codes as the congruence matrices (see below).

Between each set of five techniques for the oblique solutions and between each set of four techniques for the orthogonal solutions, congruence matrices were calculated (within each column of Table 1). The method for obtaining such matrices

was described in the Materials and Methods section. Within a set of solutions, pigeon-4 for example, there are ten congruence matrices for the oblique solutions: CFA versus PFA, ICFA, MLFA and AFA; PFA versus ICFA, MLFA and AFA; ICFA versus MLFA and AFA; and MLFA versus AFA. There were six congruence matrices for the orthogonal solutions: PFA versus ICFA, MLFA and AFA; ICFA versus MLFA and AFA; and MLFA versus AFA. No comparisons were made between orthogonal and oblique solutions to reduce computer time. These results are shown in Tables 2 to 10 as congruence matrices.

The congruence coefficients are coded into nine classes, as follows: 0.851-1.000, 4; 0.701-0.850, 3; 0.551-0.700, 2; and 0.400-0.550, 1. Minuses were used if the coefficients were negative; those less than 0.400 in absolute value were coded as zero. The congruence matrices show how similar pairs of factor solutions are. A large coefficient, $|c_{ij}| \geqq 0.851$, in a row or column would indicate congruence between two factors. There may be in addition lower congruence coefficients in the same row or column due to the fact that the factors are correlated. A blank row or column or one with low coefficients, $|c_{ij}| < 0.851$, will here be considered to indicate that the two solutions found different factors. How different two factors are depends upon the value of the congruence coefficients. See Table 2 for an illustration of the congruence matrices resulting from one solution for a data set.

The Pigeon Data Set

Three sets of oblique factor solutions with 4, 5 and 6 factors were calculated from the pigeon data. The congruences are shown in Table 2.

A factor by factor analysis of the PFA factor matrix (Table 12; Figs. 2, 4) follows. The first factor is related to flight.

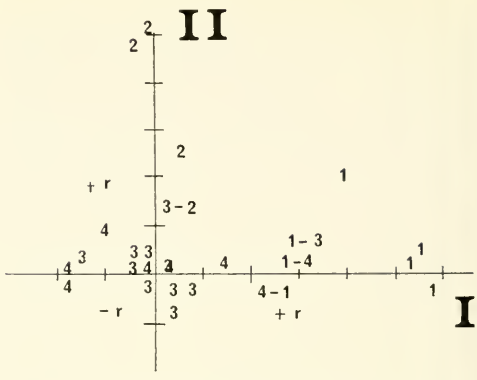

FIG. 4. An example of a factor solution giving readily interpretable factors. The numbers represent the positions of the variables in the factor space. Each variable is identified by the number of the factor with which it was associated, so that variables associated with factor I are plotted as 1's, and so on. In addition, variables associated with two factors are plotted as two numbers, e.g., 4-1 represents a variable loading highest on factor IV, but also having a fairly high loading on factor I. Factor I is the abscissa and factor II is the ordinate. Vertical and horizontal bars represent 0.1 unit of correlation. The variables are plotted onto the first two rotated factor axes. Although this was an oblique rotation, factors I and II were essentially orthogonal.

The variables with high loadings are interorbital width, maximum width of glenoid fossa, and three sternum characters. Another character, the length of the scapula, has low loadings with the flight factor and also with the length factor. The second factor loads on only three characters: length of skull and beak, height of occiput, and length of lower jaw. This was identified as a skull factor. The third factor loads on all bone lengths; and the fourth factor affects all bone widths, albeit mostly with low loadings. This implies that bone widths do not covary as consistently as do bone lengths, head lengths, and characters affecting flight performance. The flight factor and skull factor are each correlated with the length factor, implying that all covary in a similar fashion. The flight and skull factors are not intercorrelated. The length and width factors are correlated, while width is orthogonal (uncorrelated) to the other factors.

The above factors were found by PFA, CFA, and AFA. AFA tends to have lower (in absolute value) factor loadings than the two former methods. ICFA gives results similar to those of the other methods, except for many loadings near zero, so that one of its factors was difficult to identify (jaw and head length factor). The MLFA solution (the MLFA factor matrix is shown in Table 13 as an example of an analysis giving "poor" results) has three of the above factors and repeated the jaw and head length factor. It has more loadings near zero as well.

The four factor orthogonal solutions are essentially similar for all methods (the PFA solution is shown in Table 14). The factors are: the flight factor, a combination of the jaw-head length and bone width factors, a combination of the bone length and bone width factors, and a repetition of the jaw-head length factor. This meant that the congruence matrices (Table 2) between different methods tended to have high numbers in almost every row and column (due to the overlapping of the factors). These results seemed peculiar, so the analysis was repeated to check for computational errors and none were found. ICFA has near zero loadings and AFA has a few near zero loadings for one factor.

The five factor oblique solutions (Table 3) include the above four factors and a head factor of orbit and skull size in CFA, PFA and AFA. This new factor is not of great interest, since it simply includes two characters already associated with one of the four factors. This implies that the four factor solution is best. ICFA gives similar results for the four factors described above and has very low loadings, making the fifth factor uninterpretable. AFA has low loadings compared to CFA and PFA. MLFA did not converge; i.e., $\mathbf{H}^2$ for each succeeding interation did not become more similar.

The six factor oblique solution (Table 4) clearly has too many factors. All solutions have near zero loadings for all the factors and different variables loading on the fifth and sixth factors. ICFA, as with the other solution, has lower loadings (in absolute value) than the other methods. The results of MLFA make no sense when compared to the other solutions; i.e., the factors have no apparent simple biological interpretation.

The Fish Data Set

Three sets of oblique factor solutions were calculated from the fish data: 4, 5 and 6 factors. The congruences are shown in Table 5.

An analysis of the CFA factor matrix, character by character (Table 15), follows. The first factor consists of length characters, which include the majority of the characters of the study. It represents size, since fishes of all sizes were included. The second factor includes mouth part characters and a few head characters and is related to feeding, as well as to characteristics that reflect among-group variation. These characters distinguish one group, *Rhinichthys cataractae* (see Materials and Methods section), from the other two groups. The third factor consists of pelvic and pectoral fin ray counts; its interpretation is not clear. The fourth factor loads on width of frenum, width at pelvic fin origin, number of lateral line scales, number of vertebrae, and color characters. These characters distinguish *Richardsonius balteatus* from the other two groups. The mouth part factor is correlated with the pelvic and pectoral fin ray counts factor and with the fourth factor. The third and fourth factors are not correlated. These above CFA factors were also found by PFA and AFA.

The congruences for the four factor oblique solutions are shown in Table 5. The AFA factor matrix, essentially the

same as the CFA solution, is shown in Table 16. MLFA is similar to the other methods, but has many loadings near zero so that ray counts factor is difficult to identify. ICFA also has low loadings.

The orthogonal methods were carried out for the five-factor solution only (Table 6). The AFA orthogonal factor matrix is shown in Table 17. The above four factors resulted, as did a factor of all low loadings. CFA and PFA give similar results to AFA. ICFA has low loadings. By MLFA only three factors were found, since two are of all low loadings.

The five and six factor oblique solutions (Tables 6 and 7) seemed to yield too many factors, since (1) different solutions give different factors, V and VI; and (2) these new factors are divisions of the factors listed above. As before, MLFA and ICFA give poor results due to their loadings near zero.

The Complete Lizard Data Set

From this data set seven factors (Table 8) were computed. It turned out, however, to require fewer factors than the reduced data set. In retrospect, it appears that there are fewer suites of characters which covary within a data set when the samples become more heterogeneous.

The seven factor oblique solutions gave results which were very difficult to interpret, because of over extraction of factors. No method gave appreciably lower loadings than any other, but all have loadings near zero—the largest number of loadings, $|c_{ij}| \geqq 0.40$, is not more than 20 (out of 130 variables). Four oblique factors were found consistently by all five methods. The remaining three factors sometimes overlap between methods, but never over all the methods—e.g., a factor labeled III by CFA is not congruent with factors found by any other method, while one labeled VII by PFA was also found by AFA and MLFA. On the basis of the earlier results in the fish and pigeon data, it would seem that a four factor solution should give better results and that the oblique factors were difficult to interpret due to this over extraction of factors. In the orthogonal solutions, only the first four factors had high loadings, and all the methods gave similar results. This would indicate that a four factor solution would be adequate. For this reason, the data set was re-analyzed by CFA and four factors were extracted and rotated by MTAM. The factors are: scale counts on the head, lengths and widths of body and limb measurements; scale counts on the legs and feet; scale counts on the head and feet, and scale sizes; and scale type and sizes. None of these are similar to the congruent five factors found in the reduced data set, indicating that the pattern of variation in the complete set is different from that within the sceloporines alone. Owing to the many loadings near zero in the oblique solutions, there was little similarity between the orthogonal and the oblique seven factor solutions.

The Reduced Lizard Data Set

The oblique results from the reduced data set (Table 9) are somewhat different from the previous results, since ICFA, CFA, PFA and MLFA give similar results on this set. Five of the oblique factors found are: body scale counts, head scale characters, and femoral pore characters; head and body scale counts different from the previous ones, and foot scale characters; widths and scale sizes; scale counts on the body and scale types; and lengths and scale counts. A sixth factor differs for different methods and is associated with 9 to 13 characters, depending upon the factoring technique. The factors were almost entirely intercorrelated from 0.30 to 0.40 in absolute value. All the factors had similar loadings; i.e., there was no method which had factors with

loadings near zero. The results of AFA were fairly different from all the others.

The orthogonal solutions found by ICFA, PFA and MLFA are nearly the same. The AFA solution is different for two factors. Four of the orthogonal factors are essentially the same as those found by the oblique solutions. Again, all the factors had a fair number of characters associated with them.

The Fish Distribution Data Set

The interpretation of the oblique fish distribution factors (Table 10) is discussed in detail by Smith and Fisher (1970). The solutions for these interpretations were PFA and CFA which were found to be congruent, except for one factor, agreeing with the results shown in the congruence tables. ICFA, CFA, PFA and MLFA are congruent for all seven factors, while AFA is congruent for only six. The two "new" factors found by AFA were analyzed by Smith (pers. comm.) and found not to be interpretable in terms of what is known about the fish distributions. No method gave factors with appreciably lower loadings than the other methods. The eight different factors found by the various methods are different subsets of the seven factors in common to the different techniques. For example, the eighth CFA factor is a subset of the prairie and plains stream fishes. These are fishes from the same area, but found only in cold spring areas left over from earlier geological times. Fishes are found to be clearly from within one group or the other (that is, either widespread or restricted) as well as intermediate between the two (that is, not clearly part of the widespread distributions or part of the restricted distributions, but intermediate). The eighth PFA factor is found to be a slightly different arrangement of the fishes found in southern Kansas. This same pattern of the eighth factor being a subset of another factor is repeated by ICFA and MLFA. In summary, the eighth factor for the different methods is simply a subdivision of a larger factor. These subgroups were shown in two cases to have biological interpretations, but they clearly should not be considered to be patterns as important as the other, larger ones (i.e., those associated with more variables).

The orthogonal solutions are all congruent (AFA less than the others); no method gives lower loadings than any other; and the factors are the same as the oblique factors, but for one exception. This was the oblique factor differing in various oblique solutions. AFA, which gives the poorest results in the oblique solutions, also yields the poorest results in the orthogonal solutions.

DISCUSSION

Factoring Techniques

These can be discussed from the standpoint of several criteria. Is there a technique which is uniformly best in that it always gives better results than any of the other techniques? Here the concept of simple structure (Thurstone, 1947) is helpful; i.e., no factors with all low loadings ($|f_{ij}| < 0.4$) and few with variables loading on one or more other factors (due to rows with high loadings($|f_{ij}| \geqq 0.4$) on two or more factors). An example of a data set giving good simple structure is shown in Figure 4.

A less rigorous criterion than simple structure is that although a method may not be uniformly best, it may be consistent; i.e., it gives good results more often than any other technique. Another aspect to consider is robustness; i.e., are the methods adversely affected by the wrong number of factors or violations of the basic assumptions of the technique. This is an important consideration, since some data, e.g., the biodistributional data, may

be discrete rather than continuous and not fit the assumptions of the methods.

ICFA usually gave loadings near zero when compared with the other methods. Only with the fish distributions and reduced lizard data did it give good results. It was certainly not uniformly best; neither was it consistently good. In addition, it was not particularly robust, giving poor results for the smaller data sets which fit poorly to the assumptions of a population of variables and observations.

CFA and PFA, although not uniformly best, consistently gave better results. These techniques rarely had factors empty due to all loadings near zero and gave matrices with good simple structure. The two methods were not robust to the extraction of too many factors, since they gave solutions with factors with all low loadings ($|f_{ij}| < 0.4$) under these conditions. However, they were robust in terms of both continuous and discrete data.

AFA, like CFA and PFA, often gave good results, but less consistent than the two latter methods. In addition it lacked robustness for the condition of too many factors and gave poor results for the discrete fish distribution data.

MLFA was consistently poor. Only when most of the techniques gave good results, did it also give good results.

Therefore, CFA and PFA were both uniformly best and the most robust for different types of data.

Another way to consider the results is in terms of the congruence tables. These are summarized in Table 11, calculated as follows:

(1) A congruence table showing two methods to be completely congruent would have 4 or –4 once in each row or column, indicating the same factors were found by both methods.

(2) Counts were made for the number of counts different from four in a particular congruence table. For example:

	I	II	III	IV
I	3 (1)	0	0	0
II	0	–2 (2)	0	0
III	0	0	4 (0)	–2 (2)
IV	0	–1 (1)	1 (1)	0 (4)

The elements in parenthesis give the counts for missing or extra values, giving a total of eleven counts.

A high count for a particular method means that the factors computed are the least congruent to the factors of the other techniques. A low count means the converse. Since it is not possible to know in advance which technique will give the best results, the technique which consistently gives low counts, i.e., factors similar to those which were found most often by all methods, can be considered best. The last two lines of Table 11 are summaries of the number of times a particular technique gave factors which were the most like all factors found. The first (summary I) is for all data, and the second (summary II) does not include solutions where it was obvious that too many factors were extracted, i.e., the pigeon and fish data with five and six factors.

Examination of Table 11 shows that for orthogonal as well as oblique solutions PFA and CFA gave the best results in terms of solutions with factors which were the least different from those found by all methods. Using the criterion of low counts (as an indication of good results), when AFA gave good results ICFA and MLFA often gave poorer results. CFA and PFA were then most like AFA. When ICFA and MLFA gave good results, AFA often gave poor results. In such cases, CFA and PFA were most like ICFA and MLFA. MLFA often gave poor results, while all the others gave good results. For example, in the pigeon data for four oblique factors, PFA has 12 counts, CFA has 13, AFA has 18, ICFA has 18, and MLFA has 39. In the complete lizard data, for an oblique solution with an overextraction of factors, MLFA has 77 counts, AFA has 81, CFA has 82,

PFA has 91, and ICFA has 101. The times when methods other than CFA or PFA had lower counts were usually when too many factors were extracted (the fish data for 5 and 6 factors, the pigeon data for 5 and 6 factors, and the complete lizard data).

The results of this study warrant the following recommendations. The statistical factor analyses, although based upon stronger theoretical considerations, are at best a compromise. Most data sets are based upon samples of both variables and observations; this means that they violate the basic assumptions of each of these methods (shown in Fig. 1). The nonstatistical factor analyses do not have the statistical basis of the former methods, but make no assumptions about populations or samples. No compromise is necessary in a theoretical sense with regard to the more commonly analyzed data sets, where both the variables and the observations, or OTUs, are samples rather than populations. The nonstatistical methods are not sensitive to groups of variables with very high or very low communalities. This represents their computational and theoretical advantages; i.e., fewer computations are necessary and the data do not violate their assumptions. It follows that either CFA or PFA is the recommended technique.

Orthogonal Versus Oblique Rotations

In the pigeon and fish data sets, oblique rotation was clearly superior. This solution gave more interpretable factors (pigeon data) or was equivalent to the orthogonal rotation (fish data). In the larger data sets, certain problems occurred. The oblique solutions for those factors associated with a small number of variables were not independent of factoring technique. Since the orthogonal rotations were independent of the factor analytic technique, it is clearly useful to attempt both an orthogonal and an oblique rotation. This is especially true since the Varimax rotation was a good indicator of the "correct" number of factors. It simply had no loadings when too many factors were extracted. I later attempted to rotate the Varimax solution by MTAM because the Varimax solutions were congruent for different factor techniques, while the MTAM results differed. This approach was not useful, since (as was to be expected) the oblique results were the same.

MTAM does have certain advantages: it will give the same results as Varimax when the biological patterns are orthogonal; when the oblique and orthogonal solutions are similar, some of the factors may be slightly correlated, giving an estimate of the covariation in biological factors; and, theoretically, biological factors should often be correlated. The disadvantage of MTAM is that its results are not independent of factoring technique for the wrong number of factors or for factors associated with too few variables.

On the basis of this study, a recommended approach would be to try both rotational techniques and compare the results.

Considerations of Computer Time

The fastest method was CFA, followed by PFA and ICFA, with AFA and MLFA the slowest. In the smaller data sets (pigeon data with 26 variables and fish data with 39 variables), the time difference was insignificant for the different methods. In the larger data sets, with more than 100 variables, all methods other than centroid were significantly slow; so that, in light of the earlier conclusions, CFA analysis is clearly the recommended technique. Computer time for rotation is independent of the factor extraction technique. Relative computer costs and time for the GE-635 Computer are shown in Table 18.

Number of Factors

The best solution with regard to the number of factors seems to depend upon the following criteria (see also Sokal, 1959):

(1) Rohlf's (unpubl.) method: Plot on log-log paper the sum of the eigenvalues against the factor number and note the breaks in the line. This is a good initial estimate of the number of factors.
(2) An MTAM oblique solution having a substantial number of loadings near zero for all factors indicates too many factors.
(3) A Varimax orthogonal solution having factors with most loadings near zero also indicates too many factors.

If two or three solutions were attempted, the above criteria could help to decide how many factors to extract. Kaiser's criterion (Kaiser and Caffrey, 1965) of extracting factors with eigenvalues greater than 1.0 was found not to be very useful. In the pigeon data, this method would have suggested three factors which would have been one too few factors; while in the complete lizard data, eleven factors would have been extracted when in fact for the seven factor solution there were three factors too many.

In light of the different answers given by MTAM from the different techniques, solutions containing factors with few loadings should be looked upon with suspicion. Apparently, factors with few high loadings in an oblique solution are highly dependent upon the technique, while those with many high loadings are independent of the technique. This means that an oblique solution with factors with few high loadings, compared to the other factors of the solution, should be looked upon as possibly arbitrary. This is especially true in data sets of heterogeneous samples or large numbers of variables.

The Communalities

The number of iterations necessary to stabilize the communalities was found to be at least five. In the larger data sets, convergence was faster than in the smaller ones. As predicted, the communalities differed when different numbers of factors were extracted, although those variables with low communalities still had low communalities when one further factor was extracted.

ICFA uses the multiple correlation coefficients for the communalities. Even when this method gave good results (as defined above), the communalities calculated from the factor matrix differed considerably from the multiple correlations—in some cases higher and, in other cases, lower re-estimates were obtained.

The Effect of Different Kinds of Data on the Factor Solution

The data of the present study represent examples of some of the various kinds which are encountered in the field of systematics and ecology. In some cases, the simple structure factor matrices (MTAM rotated matrices) observed in this study had reasonable biological interpretation. Sokal, Daly and Rohlf (1961) discussed in some detail whether or not the concept of simple structure is a valid way of looking at nature. They concluded that, despite their misgivings about the concept, the simple structure factor matrices were invariably more interpretable than either the unrotated CFA or PFA factor matrices. In the present study, only the final rotated factor matrices were interpreted. Some data sets gave clearly interpretable simple structure factor matrices, while others gave those which were far less interpretable. This was clearly a function of the samples, or OTUs, on which the specific variables were measured.

The pigeon data set analyzed in this

study represents morphometric data from a single homogeneous population. This means that the observed correlations should reflect patterns of covariation among individuals, such as those due to size, sex, environmental effects on development, genetic linkage groups, and pleiotropy. Furthermore, bone lengths and bone widths, for example, may covary to produce two separate factors which may be correlated with each other owing to a similar relationship to general size. The factors found in the pigeon data were, in fact, interpreted as the above sort of patterns: bone lengths, bone widths, skull characters, and flight characters. Correlation among these factors was demonstrated by oblique rotation to simple structure, but its origin is found in the morphogenetic patterns affecting this character suite.

The fish data represent three groups with similar within-group variation. Since the total variation was found to be oblique to the within-group and among-group variation, the factors could be expected to be of three kinds: among-group, within-group, or mixed. Factors based on among-group variation (e.g., among species), unlike factors based on within-group variation, may not give easily interpretable factors. In this case, the factors reflect variation at the population level; that is, some trend between populations which will, in most cases, not be interpretable at the level of the individual. The results from the fish data are intermediate between those from a single population, such as the pigeon data, and those from several populations, such as the lizard data. The factors include among-group characters separating the three populations, within-population characters common to the three groups, and trophic and head structures related to feeding as well as among-population differences.

The lizard data were measured from several populations, so that the total variation represents some within- but mostly among-group variation. In addition, the variation within and among groups was not investigated for similarities in direction. This means that the observed correlations represent a mixture of variation between groups in addition to the kind of variation described for the pigeon data. Between-group variation will be greatly affected by unknown events in their evolutionary history and by choice of groups included in the study. The variation is made more complicated if the within-group variation is not the same in the different groups. The kinds of patterns involved in among-group variation might be called taxonomic or evolutionary patterns, since they represent correlations which are in part genetic and in part artificial. A different definition of the sceloporines or the iguanines would necessarily mean different groups would be included and, therefore, different correlations observed. In the complete lizard data set most of the variation was among groups. For this reason, the factors were probably a reflection of variation between populations. One factor was related to scales of the legs and feet. Common scale variation in lizards of these very different groups is clearly not due to a common genetic pool, but may be related to similarities of selection of the different groups and their common evolutionary background. The genera included are all from arid and rocky areas; and the factors possibly reflect adaptation to this environment, rather than to characters possessed by reason of common ancestry.

The fish distribution data represent discrete presence or absence distributional information and continuous environmental variables, both part of a single logical unit —the distribution of fishes and their environment in Kansas. Although not a single homogeneous group in the sense of the pigeon population, the samples con-

sisted of all fish distributions in all drainage units in Kansas. Because the model involved relatively complete samplings, readily interpretable results might have been expected. The correlations between fish distributions gave factors which were found by Smith and Fisher (1970) to be related to ecology, historical geological events, and the recent evolutionary history of the species of fishes concerned.

Implications for Future Studies

It is clear from the results of this study, as well as from previous studies, that factor analysis is a useful method for the investigation of covariation in biological data. It was shown here that, for morphometric data, factor analysis gives a reasonable biological interpretation when the samples are from a single population or from the among-groups or between-groups correlation matrices for populations with similar within and total populational variation. For data with few variables (less than 60), the technique of factor analysis used is of particular importance. If the data do not meet the assumptions required by a particular statistical factor analysis, CFA or PFA would be the preferred technique. Since, however, computational procedures for data matrices of this size are inexpensive, there is no reason why both statistical and nonstatistical factor solutions could not be obtained. In data sets with many variables (more than 60), all techniques give similar results and a CFA or PFA solution is sufficient.

Another use of factor analysis which was investigated in this paper was analysis of a mixture of discrete and continuous data for investigating biogeographic patterns. Smith and Fisher (1970) found factor analytic results from a biogeographic study including environmental variables to be readily interpretable and it was shown above that the results were fairly independent of factoring technique.

Ecologists and systematists investigating situations that are multivariate in nature should be encouraged to use multivariate techniques of investigation. If the problems and the data are compatible with the requirements outlined above, then factor analysis should be used.

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Table 1. A listing of all rotated solutions from this study.

Data sets:	Pigeon			Fish			Complete Lizard	Reduced Lizard	Fish Distributions
No. of factors:	4	5	6	4	5	6	7	6	8
Techniques of Factor Analysis									
CFA	M	M	M	M	M	M	M	M	M
PFA	M,V	M	M	M	M,V	M	M,V	M,V	M,V
ICFA	M,V	M	M	M	M,V	M	M,V	M,V	M,V
MLFA	M,V	M	M	M	M,V	M	M,V	M,V	M,V
AFA	M,V	M	M	M	M,V	M	M,V	M,V	M,V

M means rotation by MTAM, V by Varimax. The rows are the factor techniques and the columns show the data sets and the number of factors.

TABLE 2. Congruence matrices for the pigeon data, four oblique and four orthogonal factors.

		OBLIQUE SOLUTIONS				ORTHOGONAL SOLUTIONS			
		I	II	III	IV	I	II	III	IV
					CFA				
	I	4	0	0	0				
PFA	II	0	4	0	0				
	III	0	0	4	0				
	IV	0	0	0	4				
	I	4	0	0	0				
ICFA	II	0	2	0	0				
	III	0	0	4	0				
	IV	0	0	0	4				
	I	0	4	0	0				
MLFA	II	4	0	0	0				
	III	3	1	0	0				
	IV	0	0	4	0				
	I	4	0	0	0				
AFA	II	0	2	0	0				
	III	0	0	4	0				
	IV	0	1	0	4				
					PFA				
	I	4	0	0	0	4	3	3	2
ICFA	II	0	2	0	0	–3	–4	–3	–2
	III	0	0	4	0	–3	–3	–4	–2
	IV	0	0	0	4	–1	–2	0	–3
	I	0	4	0	0	4	3	3	2
MLFA	II	4	0	0	0	–3	–3	–4	–2
	III	3	2	0	0	–3	–4	–3	–2
	IV	0	0	4	0	2	2	2	4
	I	4	0	0	0	4	3	3	2
AFA	II	0	3	0	0	–3	–4	–3	–2
	III	0	0	4	0	3	2	4	1
	IV	0	0	0	4	0	0	0	2
					ICFA				
	I	0	2	0	0	4	–3	–3	–1
MLFA	II	4	0	0	0	–3	3	4	1
	III	3	2	0	0	–3	4	3	2
	IV	0	0	4	0	3	–2	–2	–3
	I	4	1	0	0	4	–3	–3	–1
AFA	II	0	2	0	0	–3	4	3	2
	III	0	0	4	0	3	–3	–4	0
	IV	0	0	0	4	0	0	0	–2
					MLFA				
	I	0	2	0	0	4	–3	–3	3
AFA	II	4	0	0	0	–3	3	4	–2
	III	4	1	0	0	3	–4	–3	2
	IV	0	0	4	0	0	0	0	2

Congruences are coded into nine classes: 4 (0.851-1.000), 3 (0.701-0.850), 2 (0.551-0.700), 1 (0.400-0.550). Minuses are used if the congruences are negative. Those < 0.400 in absolute value are coded as 0.

TABLE 3. Congruence matrices for the pigeon data, five oblique factors.

		I	II	III	IV	V
				CFA		
	I	4	0	0	0	0
	II	0	2	3	0	0
PFA	III	1	4	0	0	0
	IV	0	0	0	4	0
	V	0	0	0	0	4
	I	0	0	4	0	0
	II	4	0	0	0	0
ICFA	III	0	0	0	0	2
	IV	0	0	0	4	0
	V	1	0	0	0	4
	I	4	0	0	0	0
	II	0	2	3	0	0
AFA	III	1	4	0	0	0
	IV	0	0	4	0	0
	V	0	0	0	0	4
				PFA		
	I	0	4	0	0	0
	II	4	0	2	0	0
ICFA	III	0	0	0	0	2
	IV	0	0	0	4	0
	V	0	0	0	0	4
	I	4	0	1	0	0
	II	0	4	1	0	0
AFA	III	1	1	4	0	0
	IV	0	4	0	0	0
	V	0	0	0	0	4
				ICFA		
	I	0	4	0	0	0
	II	4	0	0	0	0
AFA	III	0	2	0	0	0
	IV	4	0	0	0	0
	V	0	0	2	0	4

For explanation of codes, see footnote of Table 2.

TABLE 4. Congruence matrices for the pigeon data, six oblique factors.

		I	II	III	IV	V	VI
					CFA		
	I	0	4	0	1	0	0
	II	0	1	0	4	0	0
PFA	III	4	0	0	1	0	0
	IV	0	0	2	0	0	0
	V	0	0	0	0	4	0
	VI	0	0	0	0	0	4
	I	0	4	0	0	0	0
	II	0	0	0	3	0	0
ICFA	III	4	0	0	1	0	0
	IV	0	0	1	0	4	0
	V	0	0	0	0	0	0
	VI	0	0	0	0	0	4

TABLE 4. (concluded)

		I	II	III	IV	V	VI
					CFA		
	I	4	0	0	2	0	0
	II	4	0	0	2	0	0
MLFA	III	0	0	0	0	0	0
	IV	0	0	0	0	2	2
	V	0	0	0	0	3	0
	VI	0	0	0	0	4	0
	I	0	4	0	1	0	0
	II	0	0	0	4	0	0
AFA	III	4	0	0	1	0	0
	IV	0	4	0	0	0	0
	V	0	0	0	0	4	0
	VI	0	0	0	0	0	4
					PFA		
	I	4	0	0	0	0	0
	II	0	3	0	0	0	0
ICFA	III	0	0	4	0	0	0
	IV	0	0	0	1	4	0
	V	0	0	0	0	0	0
	VI	0	0	0	0	0	4
	I	0	1	4	0	0	0
	II	0	2	4	0	0	0
MLFA	III	1	0	0	0	0	0
	IV	0	0	0	2	1	2
	V	0	0	0	0	3	0
	VI	0	0	0	0	4	0
	I	4	1	0	0	0	0
	II	0	4	0	0	0	0
AFA	III	0	0	4	0	0	0
	IV	4	0	0	0	0	0
	V	0	0	0	0	4	0
	VI	0	0	0	0	0	4
					ICFA		
	I	0	1	4	0	0	0
	II	0	1	4	0	0	0
MLFA	III	0	0	0	0	0	0
	IV	0	0	0	2	0	2
	V	0	0	0	3	0	0
	VI	0	0	0	3	0	0
	I	4	0	0	0	0	0
	II	0	2	0	0	0	0
AFA	III	0	0	4	0	0	0
	IV	4	0	0	0	0	0
	V	0	0	0	4	0	0
	VI	0	0	0	0	0	4
					MLFA		
	I	0	0	0	0	0	0
	II	1	2	0	0	0	0
AFA	III	4	3	0	0	0	0
	IV	0	0	1	0	0	0
	V	0	0	0	2	3	4
	VI	0	0	0	2	0	0

For explanation of codes, see footnote of Table 2.

TABLE 5. Congruence matrices for the fish data, four oblique factors.

		I	II	III	IV
			CFA		
	I	1	2	2	−2
PFA	II	4	0	0	0
	III	0	0	4	0
	IV	0	0	0	4
	I	0	4	0	0
ICFA	II	1	2	2	−2
	III	0	0	4	0
	IV	0	0	0	4
	I	4	0	0	0
MLFA	II	0	4	0	−1
	III	0	1	2	0
	IV	0	0	0	4
	I	1	2	2	−2
AFA	II	4	0	0	0
	III	0	0	4	0
	IV	0	0	0	4
			PFA		
	I	2	0	0	0
ICFA	II	4	1	1	−2
	III	1	0	4	0
	IV	−2	0	0	4
	I	1	4	0	0
MLFA	II	3	0	0	−1
	III	3	0	1	−1
	IV	−2	0	0	4
	I	4	1	1	−2
AFA	II	1	4	0	0
	III	1	0	4	0
	IV	−2	0	0	4
			ICFA		
	I	0	1	0	0
MLFA	II	4	3	0	−1
	III	1	3	1	0
	IV	0	−2	0	4
	I	2	4	1	−2
AFA	II	0	1	0	0
	III	0	1	4	0
	IV	0	−2	0	4
			MLFA		
	I	1	3	3	−2
AFA	II	4	0	0	0
	III	0	0	1	0
	IV	0	−1	−1	4

For explanation of codes, see footnote of Table 2.

Table 6. Congruence matrices for the fish data, five oblique and five orthogonal factors.

		OBLIQUE SOLUTIONS					ORTHOGONAL SOLUTIONS				
		I	II	III	IV	V	I	II	III	IV	V
						CFA					
	I	0	4	0	0	0					
	II	3	0	0	0	0					
PFA	III	4	0	0	0	0					
	IV	0	0	4	0	3					
	V	0	0	0	3	−4					
	I	4	0	0	0	0					
	II	0	4	0	0	0					
ICFA	III	0	0	0	−2	3					
	IV	0	0	3	0	0					
	V	0	0	0	3	−3					
	I	0	4	0	0	0					
	II	1	0	0	0	−1					
MLFA	III	0	0	0	−1	3					
	IV	0	0	1	2	0					
	V	−1	0	0	−2	4					
	I	0	4	0	0	0					
	II	3	0	0	0	0					
AFA	III	0	0	4	0	0					
	IV	0	0	3	0	0					
	V	0	0	0	3	−4					
						PFA					
	I	0	3	4	0	0	4	−1	−1	0	0
	II	4	0	0	0	0	−1	4	0	0	0
ICFA	III	0	0	0	0	−3	−1	0	4	0	0
	IV	0	0	0	4	0	0	0	0	4	0
	V	0	0	0	0	4	0	0	0	0	−2
	I	4	0	0	0	0	4	−1	−1	0	0
	II	0	2	1	0	0	−1	4	1	0	0
MLFA	III	0	0	0	0	−3	−1	0	4	0	0
	IV	0	1	0	2	0	0	0	0	0	1
	V	0	0	−1	0	−4	0	0	0	−3	0
	I	4	0	0	0	0	4	−1	−1	0	0
	II	0	4	3	0	0	−1	4	0	0	0
AFA	III	0	0	0	4	0	−1	0	4	0	0
	IV	0	0	0	4	0	0	0	0	−4	0
	V	0	0	0	0	4	0	0	0	0	4
						ICFA					
	I	0	4	0	0	0	4	−1	−1	0	0
	II	0	0	0	1	0	−1	4	1	0	0
MLFA	III	0	0	4	0	−2	−1	0	4	0	1
	iV	0	0	0	3	0	0	0	0	0	−4
	V	0	0	3	0	−4	0	0	0	−4	0
	I	0	4	0	0	0	4	−1	−1	0	0
	II	3	0	0	0	0	−1	4	0	0	0
AFA	III	0	0	0	3	0	−1	0	4	0	1
	IV	0	0	0	4	0	0	0	0	−4	0
	V	0	0	−3	0	4	0	0	0	0	−1
						MLFA					
	I	4	0	0	0	0	4	−1	−1	0	0
	II	0	2	0	1	0	−1	4	0	0	0
AFA	III	0	0	0	2	0	−1	1	4	0	0
	IV	0	0	0	3	0	0	0	0	0	0
	V	0	0	−3	0	−4	0	0	0	0	3

For explanation of codes, see footnote of Table 2.

TABLE 7. Congruence matrices for the fish data, six oblique factors.

		I	II	III	IV	V	VI
				CFA			
	I	4	0	0	0	0	0
	II	0	3	3	0	1	0
PFA	III	0	3	4	0	0	0
	IV	0	1	0	3	0	0
	V	0	0	0	0	4	0
	VI	0	0	0	1	0	–4
	I	4	0	0	0	0	0
	II	0	3	4	0	0	0
ICFA	III	0	1	0	3	0	0
	IV	0	0	0	2	2	–1
	V	0	0	0	0	3	0
	VI	0	0	0	0	0	3
	I	3	0	0	1	0	0
	II	0	3	4	0	0	–1
MLFA	III	0	3	1	3	0	0
	IV	0	0	0	1	0	–1
	V	0	2	0	2	2	0
	VI	0	0	0	0	1	–3
	I	0	4	3	1	0	0
	II	4	0	0	0	0	0
AFA	III	0	3	4	0	0	0
	IV	0	0	0	3	0	0
	V	0	0	0	0	4	0
	VI	0	0	0	0	0	–4
				PFA			
	I	4	0	0	0	0	0
	II	0	2	4	0	0	0
ICFA	III	0	0	0	4	0	0
	IV	1	0	0	0	1	1
	V	0	1	0	0	4	0
	VI	0	0	0	0	0	–4
	I	3	0	0	0	0	0
	II	0	2	4	0	0	0
MLFA	III	0	2	1	3	0	0
	IV	2	0	0	0	0	1
	V	0	1	0	1	3	0
	VI	0	0	0	0	1	4
	I	0	4	3	0	0	0
	II	4	0	0	0	0	0
AFA	III	0	3	4	0	0	0
	IV	0	0	0	4	0	0
	V	0	1	0	0	4	0
	VI	0	0	0	0	0	4
				ICFA			
	I	3	0	1	0	0	0
	II	0	4	0	0	0	0
MLFA	III	0	1	3	0	0	0
	IV	0	0	0	3	0	0
	V	0	0	1	1	2	0
	VI	0	0	0	2	0	–3
	I	0	3	0	0	0	0
	II	4	0	0	0	0	0
AFA	III	0	4	0	0	0	0
	IV	0	0	4	0	0	0
	V	0	0	0	1	4	0
	VI	0	0	0	1	0	–4
				MLFA			
	I	0	3	3	0	2	0
	II	3	0	0	1	0	0
AFA	III	0	4	1	0	0	0
	IV	0	0	3	0	0	0
	V	0	0	0	0	3	1
	VI	0	0	0	0	0	3

For explanation of codes, see footnote of Table 2.

TABLE 8. Congruence matrices for the lizard data, seven oblique and seven orthogonal factors

		OBLIQUE SOLUTIONS							ORTHOGONAL SOLUTIONS						
		I	II	III	IV	V	VI	VII	I	II	III	VI	V	VI	VII
						CFA									
	I	2	4	0	1	0	0	0							
	II	0	2	0	0	–1	0	0							
	III	3	2	0	0	0	0	0							
PFA	IV	0	0	2	0	4	0	0							
	V	0	0	0	1	0	4	0							
	VI	0	0	0	0	0	0	4							
	VII	2	0	–2	0	0	1	0							
	I	1	1	1	0	0	0	0							
	II	0	1	3	0	1	–3	0							
	III	1	1	0	4	0	1	0							
ICFA	IV	0	2	0	0	–3	0	0							
	V	4	2	0	0	0	0	0							
	VI	0	0	2	0	0	0	0							
	VII	0	0	0	0	0	0	4							
	I	4	2	0	1	0	0	0							
	II	2	4	0	1	0	0	0							
	III	1	1	0	4	0	1	0							
MLFA	IV	0	0	2	0	4	0	0							
	V	0	0	0	1	0	4	0							
	VI	0	0	0	0	0	0	4							
	VII	2	0	–2	0	0	0	0							

Table 8. (concluded)

		OBLIQUE SOLUTIONS							ORTHOGONAL SOLUTIONS						
		I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
								CFA							
	I	1	1	1	0	0	0	0							
	II	3	2	0	0	0	0	0							
	III	0	0	2	0	4	0	0							
AFA	IV	0	0	0	0	0	0	0							
	V	0	0	0	1	0	4	0							
	VI	0	0	0	0	0	0	4							
	VII	2	0	−2	0	0	1	0							
								PFA							
	I	1	2	3	0	0	0	0	4	0	0	0	0	0	0
	II	1	0	0	1	−3	0	−1	0	4	0	−1	0	0	0
	III	2	0	0	0	1	0	0	0	0	4	0	0	0	0
ICFA	IV	2	3	1	−3	0	0	0	0	−1	0	4	0	0	0
	V	3	1	4	0	0	0	2	0	0	0	0	4	0	0
	VI	0	1	0	0	0	0	0	0	0	0	0	0	4	0
	VII	0	0	0	0	0	4	0	0	0	0	0	0	0	−4
	I	2	0	3	0	0	0	2	4	0	0	0	0	0	0
	II	4	2	2	0	0	0	0	0	4	0	−1	0	0	0
	III	1	0	0	0	1	0	0	0	0	4	0	0	0	0
MLFA	IV	0	−1	0	4	0	0	0	0	1	0	−4	0	0	0
	V	0	0	0	0	4	0	1	0	0	0	0	−4	0	0
	VI	0	0	0	0	0	4	0	0	0	0	0	0	0	4
	VII	0	0	2	0	0	0	4	0	0	0	0	0	4	0
	I	1	2	3	0	0	0	0	4	0	0	0	0	0	0
	II	2	2	4	0	0	0	2	0	4	0	−1	0	0	0
	III	0	−1	0	4	0	0	0	0	0	4	0	0	0	0
AFA	IV	0	−1	0	0	0	0	0	0	−1	0	4	0	0	0
	V	0	0	0	0	4	0	1	0	0	0	0	4	0	0
	VI	0	0	0	0	0	4	0	0	0	0	0	0	−4	0
	VII	0	0	2	0	1	0	4	0	0	0	0	0	0	3
								ICFA							
	I	1	0	1	0	4	0	0	4	0	0	0	0	0	0
	II	1	1	2	2	3	0	0	0	4	0	−1	0	0	0
	III	0	0	4	0	0	0	0	0	0	4	0	0	0	0
MLFA	IV	0	1	0	−3	0	0	0	0	1	0	−4	0	0	0
	V	0	−2	1	0	0	0	0	0	0	0	0	−4	0	0
	VI	0	0	0	0	0	0	4	0	0	0	0	0	0	−4
	VII	0	−1	0	0	2	0	0	0	0	0	0	0	4	0
	I	4	0	0	0	2	2	0	4	0	0	0	0	0	0
	II	3	0	0	1	4	0	0	0	4	0	−1	0	0	0
	III	0	1	0	−3	0	0	0	0	0	4	0	0	0	0
AFA	IV	0	0	0	0	0	0	0	0	−1	0	4	0	0	0
	V	0	−3	1	0	0	0	0	0	0	0	0	4	0	0
	VI	0	0	0	0	0	0	4	0	0	0	0	0	−4	0
	VII	0	−1	0	0	2	0	0	0	0	0	0	0	0	−4
								MLFA							
	I	1	1	0	0	0	0	0	4	0	0	0	0	0	0
	II	3	2	0	0	0	0	2	0	4	0	1	0	0	0
	III	0	0	0	4	0	0	0	0	0	4	0	0	0	0
AFA	IV	0	0	0	0	0	0	0	0	−1	0	−4	0	0	0
	V	0	0	1	0	4	0	0	0	0	0	0	−4	0	0
	VI	0	0	0	0	0	4	0	0	0	0	0	0	0	−4
	VII	2	0	0	0	1	0	4	0	0	0	0	0	2	0

For explanation of codes, see footnote of Table 2.

TABLE 9. Congruence matrices for the reduced lizard data, six oblique and six orthogonal factors.

		OBLIQUE SOLUTIONS						ORTHOGONAL SOLUTIONS					
		I	II	III	IV	V	VI	I	II	III	IV	V	VI
								CFA					
	I	−3	0	0	2	0	0						
	II	1	3	1	0	0	0						
PFA	III	2	0	0	0	0	0						
	IV	0	0	0	0	4	0						
	V	0	0	0	0	0	4						
	VI	0	0	4	0	0	0						
	I	4	0	0	−1	0	0						
	II	0	4	0	0	0	0						
ICFA	III	0	0	4	0	0	0						
	IV	0	0	0	0	−4	0						
	V	1	0	0	−2	−1	0						
	VI	0	0	0	0	0	4						
	I	4	0	0	−1	0	0						
	II	0	4	0	0	0	0						
MLFA	III	0	0	4	0	0	0						
	IV	0	0	0	0	−4	0						
	V	1	0	0	−2	−1	0						
	VI	0	0	0	0	0	4						
	I	−3	0	0	2	0	0						
	II	0	0	3	0	0	0						
AFA	III	2	0	0	0	−1	0						
	IV	0	3	0	0	0	0						
	V	0	0	0	0	4	0						
	VI	0	0	0	3	1	1						
								PFA					
	I	−3	1	2	0	0	0	0	0	4	0	0	0
	II	0	3	0	0	0	0	1	4	0	0	0	0
ICFA	III	0	1	0	0	0	4	−1	0	0	4	0	0
	IV	3	0	0	−4	0	0	0	0	0	0	0	−4
	V	−1	0	0	−1	0	0	0	0	0	0	−4	0
	VI	0	0	0	0	4	0	4	1	0	0	0	0
	I	−3	1	2	0	0	0	0	0	4	0	0	0
	II	0	3	0	0	0	0	1	4	0	0	0	0
MLFA	III	0	1	0	0	0	4	−1	0	0	4	0	0
	IV	3	0	0	−4	0	0	0	0	0	0	0	−4
	V	−1	0	0	−1	0	0	0	0	0	0	−4	0
	VI	0	0	0	0	4	0	4	1	0	0	0	0
	I	4	0	0	0	0	0	4	0	0	−2	0	0
	II	0	0	−1	0	0	1	1	4	0	0	0	0
AFA	III	0	0	3	−1	0	0	−1	0	3	2	−1	0
	IV	0	2	0	0	0	0	1	0	0	0	0	0
	V	0	0	0	4	0	0	0	0	0	0	−3	0
	VI	0	0	0	1	1	0	0	0	−2	0	1	−3
								ICFA					
	I	4	0	0	0	1	0	4	0	0	0	0	0
	II	0	4	0	0	0	0	0	4	0	0	0	1
MLFA	III	0	0	4	0	0	0	0	0	4	0	0	−1
	IV	0	0	0	4	0	0	0	0	0	4	0	0
	V	1	0	0	0	4	0	0	0	0	0	4	0
	VI	0	0	0	0	0	4	0	1	−1	0	0	4

TABLE 9. (concluded)

		OBLIQUE SOLUTIONS						ORTHOGONAL SOLUTIONS					
		I	II	III	IV	V	VI	I	II	III	IV	V	VI
							ICFA						
	I	−3	0	0	2	−1	0	0	0	−2	0	0	4
	II	0	0	3	0	0	0	0	4	0	0	0	1
AFA	III	3	0	0	0	0	−1	3	0	1	0	1	−1
	IV	0	3	0	0	0	0	0	0	0	0	0	1
	V	0	0	0	−3	−1	0	0	0	0	0	3	0
	VI	0	0	0	0	−3	1	−2	0	0	2	−1	0
							MLFA						
	I	−3	0	0	2	−1	0	0	0	−2	0	0	4
	II	0	0	3	0	0	0	0	4	0	0	0	1
AFA	III	3	0	0	0	0	−1	3	0	1	0	1	−1
	IV	0	3	0	0	0	0	0	0	0	0	0	1
	V	0	0	0	−3	−1	0	0	0	0	0	3	0
	VI	0	0	0	0	−3	1	−2	0	0	2	−1	0

For explanation of codes, see footnote of Table 2.

TABLE 10. Congruence matrices for the fish distribution data, eight oblique and eight orthogonal factors.

		OBLIQUE SOLUTIONS								ORTHOGONAL SOLUTIONS							
		I	II	III	IV	V	VI	VII	VIII	I	II	III	IV	V	VI	VII	VIII
									CFA								
	I	4	0	0	0	0	0	0	0								
	II	0	0	0	0	0	0	0	0								
	III	0	0	0	0	2	4	0	0								
PFA	IV	0	0	4	0	0	0	0	0								
	V	0	0	0	4	0	0	0	0								
	VI	0	4	0	0	0	0	0	1								
	VII	0	2	0	0	0	0	0	4								
	VIII	0	0	0	0	2	0	4	0								
	I	4	0	0	0	0	0	0	0								
	II	0	4	0	0	0	0	0	2								
	III	0	0	0	0	0	0	0	2								
ICFA	IV	0	0	0	0	2	4	0	0								
	V	0	0	4	0	0	0	0	0								
	VI	0	0	0	4	0	0	0	0								
	VII	0	2	0	0	0	0	0	4								
	VIII	0	0	0	0	3	0	4	0								
	I	4	0	0	0	0	0	0	0								
	II	0	0	3	0	0	0	0	0								
	III	0	3	0	0	0	0	0	2								
MLFA	IV	0	0	0	0	0	4	0	0								
	V	0	0	0	4	0	0	0	0								
	VI	0	0	0	0	3	0	4	0								
	VII	0	0	0	0	2	2	0	0								
	VIII	0	2	0	0	0	0	0	4								
	I	4	0	0	0	0	0	0	0								
	II	0	0	4	0	0	0	0	0								
	III	0	0	0	4	0	0	0	0								
AFA	IV	0	0	0	0	−1	0	−1	0								
	V	0	0	0	0	0	4	0	0								
	VI	0	0	0	0	0	0	0	0								
	VII	0	0	0	0	1	0	4	0								
	VIII	0	2	0	0	0	0	0	4								

TABLE 10. (concluded)

		OBLIQUE SOLUTIONS								ORTHOGONAL SOLUTIONS							
		I	II	III	IV	V	VI	VII	VIII	I	II	III	IV	V	VI	VII	VIII
									PFA								
	I	4	0	0	0	0	0	0	0	4	0	0	−1	0	1	0	−1
	II	0	0	0	0	0	4	1	0	0	4	0	0	0	0	0	0
	III	0	2	0	0	0	0	3	0	0	0	4	0	0	0	0	0
ICFA	IV	0	0	4	0	0	0	0	0	−1	0	0	4	0	0	0	0
	V	0	0	0	4	0	0	0	0	0	0	0	0	4	0	0	0
	VI	0	0	0	0	4	0	0	0	1	0	0	0	0	4	0	0
	VII	0	0	0	0	0	0	4	0	0	0	0	0	0	0	−4	0
	VIII	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	4
	I	4	0	0	0	0	0	0	0	1	0	0	0	0	4	0	0
	II	0	0	1	3	0	0	0	0	0	4	0	0	0	0	0	0
	III	0	0	0	0	0	3	2	0	1	0	0	−4	0	0	0	0
MLFA	IV	0	0	4	0	0	0	0	0	0	0	−4	0	0	0	0	0
	V	0	0	0	0	4	0	0	0	4	0	0	−1	0	1	0	−1
	VI	0	0	0	0	0	0	0	4	0	0	0	0	0	0	4	0
	VII	0	0	2	0	0	0	0	0	0	−1	0	0	−4	0	−1	0
	VIII	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	−3
	I	4	0	0	0	0	0	0	0	4	0	0	−1	0	2	0	−1
	II	0	0	0	4	0	0	0	0	0	4	0	0	1	0	0	0
	III	0	0	0	0	4	0	0	0	0	0	−4	0	0	0	0	0
AFA	IV	0	0	0	0	0	0	0	−1	−1	0	0	4	0	0	0	1
	V	0	0	4	0	0	0	0	0	0	0	0	0	4	0	0	0
	VI	0	−1	0	0	−1	0	0	0	0	0	0	0	0	3	0	0
	VII	0	0	0	0	0	0	0	4	−1	0	0	0	−1	−1	−4	0
	VIII	0	0	0	0	0	1	4	0	0	0	0	0	0	−1	0	−2
									ICFA								
	I	4	0	0	0	0	0	0	0	1	0	0	0	0	4	0	0
	II	0	0	0	1	3	0	0	0	0	4	0	0	0	0	0	0
	III	0	3	0	0	0	0	2	0	1	0	0	−4	0	0	0	0
MLFA	IV	0	0	0	4	0	0	0	0	0	0	−4	0	0	0	0	0
	V	0	0	0	0	0	4	0	0	4	0	0	−1	0	1	0	−1
	VI	0	0	0	0	0	0	0	4	0	0	0	0	0	0	−4	0
	VII	0	0	0	2	0	0	0	2	0	−1	0	0	−4	0	1	0
	VIII	0	1	3	0	0	0	4	0	0	0	0	0	0	0	0	−3
	I	4	0	0	0	0	0	0	0	4	0	0	−1	0	2	0	−1
	II	0	0	0	0	4	0	0	0	0	4	0	0	0	0	0	0
	III	0	0	0	0	0	4	0	0	0	0	−4	0	0	0	0	0
AFA	IV	0	0	0	0	0	0	0	−2	−1	0	0	4	0	0	0	0
	V	0	0	0	4	0	0	0	0	0	0	0	0	4	0	0	0
	VI	0	0	−1	0	0	−1	0	0	0	0	0	0	0	3	0	0
	VII	0	0	0	0	0	0	0	4	−1	0	0	0	−1	−1	4	0
	VIII	0	2	2	0	0	0	4	0	0	0	0	0	0	−1	0	−2
									MLFA								
	I	4	0	0	0	0	0	0	0	2	0	1	0	4	0	0	0
	II	0	3	0	0	0	0	0	0	0	4	0	0	0	0	−1	0
	III	0	0	0	0	4	0	0	0	0	0	0	4	0	0	0	0
AFA	IV	0	0	0	0	0	−2	−3	0	0	0	−4	0	−1	0	0	0
	V	0	0	0	4	0	0	2	0	0	0	0	0	0	0	−4	0
	VI	0	0	0	0	−1	0	0	0	3	0	0	0	0	0	0	0
	VII	0	0	0	0	0	3	0	0	−1	0	0	0	−1	−4	1	0
	VIII	0	0	2	0	0	0	0	4	0	0	0	0	0	0	0	1

For explanation of codes, see footnote of Table 2.

Table 11. Counts of mismatches for diagonal matrices in congruence matrices.

	ICFA		CFA	PFA		AFA		MLFA		Table No. of Congruence Matrices
	VAR*	MTAM**	MTAM	VAR	MTAM	VAR	MTAM	VAR	MTAM	
Pigeon 4	81	18	13	82	12	72	18	91	39	2
Pigeon 5	....	32	21	....	24	....	38	....	....	3
Pigeon 6	....	46	45	....	38	....	49	....	89	4
Fish 4	....	56	27	....	38	....	40	....	44	5
Fish 5	21	41	47	20	45	22	46	24	56	6
Fish 6	....	48	57	....	48	....	42	....	71	7
Reduced Lizard 6	25	40	39	24	54	54	60	25	40	8
Lizard 7	6	101	82	6	91	8	81	8	77	9
Fish Distributions 8	25	52	52	27	38	39	51	28	55	10
Summary I	1.5	1	3	2.5	3	1	1	0	1	
Summary II	1.5	0	2	1.5	2	1	0	0	1	

Rows are the nine solutions and two summaries described in the text. Columns represent the five techniques with separate columns for oblique (MTAM) and orthogonal (Varimax) rotation.
* Varimax rotation.
** MTAM rotation.

Table 12. The factor matrix for the oblique four factor PFA solution from the pigeon data.

	I	II	III	IV
1	0	1	0	0
2	2	0	0	0
3	0	0	1	0
4	0	1	0	0
5	0	1	0	0
6	0	0	1	0
7	0	0	0	1
8	1	1	0	0
9	1	0	1	0
10	1	0	0	0
11	1	0	0	0
12	1	0	0	0
13	0	0	0	1
14	0	0	1	0
15	0	0	0	1
16	0	0	1	0
17	0	0	1	0
18	0	0	2	0
19	0	0	0	1
21	0	0	1	0
22	0	0	0	1
23	0	0	1	0
24	0	0	0	1
25	0	0	1	0
26	0	0	2	0
27	0	0	0	2

The factor loadings have been coded the same as the congruences, which are described in Table 2 (except 1 is for loadings between 0.300 and 0.550). Labels are as described in Figure 2.

Table 13. The MLFA four factor oblique solution for the pigeon data.

	I	II	III	IV
1	1	0	1	0
2	0	2	0	0
3	0	0	0	0
4	0	0	0	0
5	1	0	0	0
6	0	0	0	0
7	0	0	0	0
8	0	0	0	0
9	0	0	0	0
10	0	1	1	0
11	0	2	1	0
12	0	1	1	0
13	0	0	0	0
14	0	0	0	0
15	0	0	0	0
16	0	0	0	0
17	0	0	0	1
18	0	0	0	2
19	0	0	0	0
21	0	0	0	1
22	0	0	0	0
23	0	0	0	0
24	0	0	0	0
25	0	0	0	0
26	0	0	0	1
27	0	0	0	0

Codes for loadings and factor labels are as described in Table 2 and Figure 2. Note that 1 is for loadings between 0.400 and 0.550.

TABLE 14. The PFA four factor orthogonal solution from the pigeon data.

	Communalities	I	II	III	IV
1	3	−1	0	−1	−2
2	1	0	−2	0	0
3	0	0	0	0	0
4	0	0	0	0	0
5	3	−1	0	−1	−1
6	3	−3	0	0	0
7	2	0	−1	−2	0
8	0	0	−1	0	0
9	3	−2	−1	0	0
10	3	−1	−3	0	0
11	2	0	−2	0	0
12	1	0	−1	0	0
13	0	−1	0	−1	0
14	4	−3	0	0	0
15	2	−2	0	−2	0
16	0	−2	0	0	0
17	4	−3	0	0	0
18	4	−4	0	0	0
19	1	0	0	−1	0
21	3	−3	0	0	0
22	2	−1	0	−1	0
23	3	−3	0	0	0
24	2	−1	0	−2	0
25	1	−2	0	0	0
26	4	−3	0	0	0
27	2	0	0	−3	0

Coding for loadings and factor labels are as described in Table 2 and Figure 2.

TABLE 15. List of the 39 characters coded for the fish data and the factor matrix for the CFA four factor oblique solution.

Character I. D.	Description of Characters	I	II	III	IV
A	Standard length	3	0	0	0
B	Caudal base to dorsal fin origin	2	0	0	0
C	Caudal base to pelvic fin origin	3	0	0	0
D	Caudal base to anal fin origin	3	0	0	0
E	Head length	3	0	0	0
F	Post orbital length	3	0	0	0
G	Nasal length	0	3	0	0
H	Length of snout to end of lip	2	0	0	0
I	Length of snout to lower jaw tip	0	3	0	0
J	Eye diameter	0	−1	0	0
K	Nostril length	0	1	0	0
L	Internasal width	3	0	0	0
M	Interorbital width	3	0	0	0
N	Head width at pupil	3	0	0	0
O	Head depth at nostril	3	0	0	0
P	Head depth at pupil	2	−1	0	0
Q	Head depth at occiput	2	−1	0	0
R	Dorsal fin origin to pelvic fin origin	2	0	0	0
S	Least depth, caudal peduncle	4	0	0	0
T	Least depth, caudal peduncle at last vertebrae	3	0	0	0
U	Width of frenum	0	3	0	−1
V	Length of preopercular groove	0	−2	0	0
W	Height, nostril flap	0	2	0	0
X	Width, opercular flap	0	0	0	0
Y	Width of isthmus	0	2	0	0
Z	Width at pelvic fin origin	3	0	0	1
AA	Width between inner margin of mandibles	2	0	0	0
BB	Number of lateral line scales	0	0	0	2
CC	Number of pelvic rays	0	0	1	0
DD	Number of pectoral rays	0	0	1	0
EE	Number of vertebrae	0	0	0	−1
FF	Color pattern of sides	0	3	0	0
GG	Color pattern of caudal peduncle	0	1	0	0
HH	Color pattern of caudal fin	0	0	0	2
II	Color of peritoneum	0	0	0	3
JJ	Length of posterior chamber of swim bladder	1	−2	0	0
KK	Number of dorsal rays	0	−1	0	0
LL	Number of anal rays	0	−1	0	0
MM	Number of barbels	0	2	0	0

Codings for the loadings are given in Table 2.

Table 16. The AFA four factor oblique solution from the fish data.

	I	II	III	IV
A	0	3	0	0
B	0	2	0	0
C	0	2	0	0
D	1	3	0	0
E	0	3	0	0
F	0	3	0	0
G	3	1	0	0
H	1	2	0	0
I	1	0	0	0
J	0	0	0	0
K	2	0	0	0
L	0	3	0	0
M	0	2	0	0
N	1	3	0	0
O	0	2	0	0
P	0	1	0	0
Q	0	1	0	0
R	0	1	0	0
S	0	3	0	0
T	0	3	0	0
U	3	0	0	−1
V	0	0	0	0
W	3	0	0	0
X	2	0	0	0
Y	0	0	0	0
Z	0	3	0	1
AA	0	1	0	0
BB	0	0	0	2
CC	1	0	1	0
DD	1	0	2	0
EE	0	0	0	−1
FF	0	0	0	0
GG	0	0	0	0
HH	0	0	0	2
II	2	0	0	3
JJ	0	0	0	0
KK	0	0	0	0
LL	0	0	0	0
MM	0	0	0	0

Coding for loadings are as in Table 2. Characters are described in Table 15.

Table 17. The AFA five factor orthogonal solution from the fish data.

	Comm.*	I	II	III	IV	V
A	4	−4	0	0	0	0
B	2	−3	0	0	0	0
C	4	−4	0	0	0	0
D	3	−3	0	0	0	0
E	4	−4	0	0	0	0
F	3	−4	0	0	0	0
G	3	0	−3	0	0	0
H	4	−3	0	1	0	0
I	4	0	−4	0	0	0
J	4	−2	3	1	0	0
K	2	0	−1	0	0	0
L	4	−4	0	0	0	0
M	4	−3	1	0	0	0
N	4	−4	0	0	0	0
O	4	−3	1	0	0	0
P	4	−3	2	0	0	0
Q	4	−3	2	0	0	0
R	4	−3	2	0	0	0
S	3	−4	0	0	0	0
T	4	−4	0	0	0	0
U	4	0	−4	0	0	0
V	4	−1	3	0	0	0
W	2	0	−2	0	0	0
X	0	−1	0	0	0	0
Y	4	0	−3	−1	0	0
Z	3	−3	0	−1	0	0
AA	4	−3	0	1	0	0
BB	3	0	0	−3	0	0
CC	0	0	0	0	−1	0
DD	1	0	0	0	−2	0
EE	1	0	0	2	0	0
FF	4	0	−4	0	0	0
GG	3	0	−2	−1	0	0
HH	4	0	0	−3	0	0
II	3	0	0	−3	0	0
JJ	4	−1	3	0	0	0
KK	1	0	2	0	0	0
LL	4	0	2	2	0	0
MM	3	0	−3	0	0	0

Codings for loadings as in Table 2. Characters are described in Table 15.
* Communalities.

Table 18. The relative computing costs and central processor unit, CPU, time on a GE-635 computer for the pigeon data, four factors; and the fish distribution data, eight factors.

Technique	Pigeon (26 variables)		Fish Distribution (133 variables)	
	Relative CPU Time	Relative Total Computing Cost	Relative CPU Time	Relative Total Computing Cost
CFA	1 <	1	4	7
PFA	1 <	3	20	50
AFA	3	10	60	150*
MTAM	3	5	3	5
Varimax	1	1	1	1

The number of iterations was ten, except for five for the fish distribution AFA. In addition, the times and costs for the MTAM and Varimax rotations are shown.
* The costs for AFA may be slightly excessive, due to the methods used. A more effective method would probably make costs for AFA more like those of PFA, although still slightly higher.

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DESCRIPTIONS OF LARVAE AND KEY TO FOURTH INSTARS OF NORTH AMERICAN *PANORPA* (MECOPTERA: PANORPIDAE)

By

ANN E. BOESE

Vol. 50, No. 4, pp. 163-186 November 14, 1973

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Descriptions of Larvae and Key to Fourth Instars of North American *Panorpa* (Mecoptera: Panorpidae)

Ann E. Boese

Descriptions of Larvae and Key to Fourth Instars of North American *Panorpa* (Mecoptera: Panorpidae)[1]

Ann E. Boese[2]

ABSTRACT

A general description of the morphology of *Panorpa* larvae is given, with special emphasis on the chaetotaxy. The fourth instar larvae of thirteen North American species, *P. acuta, P. anomala, P. banksi, P. carolinensis, P. claripennis, P. flexa, P. helena, P. latipennis, P. lugubris, P. mirabilis, P. nebulosa, P. nuptialis,* and *P. subulifera,* are described in detail with a key for identifying them. Intraspecific variation of the larvae is also discussed.

INTRODUCTION

Most taxonomic studies of the Mecoptera have dealt with the adults, and little has been done on the classification of larvae. A notable exception is the work of Yie (1951) on larvae of *Panorpa* and *Neopanorpa* in Formosa. The genus *Panorpa* contains 42 species in North America, but the larvae of only four have so far been described; and only once (Mampe and Neunzig, 1965) has there been any attempt to compare and differentiate North American species in this genus. The purpose of this paper is to give a general description of the morphology of *Panorpa* larvae and detailed descriptions of several North American species, together with a key for identifying them.

HISTORICAL REVIEW

Until Brauer's work (1863) in which he studied the life history of three European species, *Panorpa communis* Linnaeus, *P. alpina* Rambur (as *variabilis*), and *P. germanica* Linnaeus (as *montana*), nothing had been done on the immature forms, and most studies of the genus *Panorpa* have concerned the adults. Larvae of the following panorpid species have since been studied: *P. communis* Linnaeus (Shiperovitsh, 1925; Steiner, 1930; Potter, 1938), *P. debilis* Westwood (Felt, 1896; Byers, 1954, 1963), *P. nuptialis* Gerstaecker (Byers, 1963; Gassner, 1963), *P. lugubris* Swederus and *P. virginica* Banks (Mampe and Neunzig, 1965), *P. klugi* MacLachlan (Miyaké, 1912), *P. falsa* Issiki (Yie, 1951), *P. maculosa* Hagen (Carpenter, 1931) and *P. germanica* Linnaeus (Potter, 1938).

Brief general descriptions of *Panorpa* larvae have been written by Packard (1883) and Peterson (1951).

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I would like to thank Dr. George W. Byers, under whose direction this study was made, for his assistance and useful comments, and for rearing and providing the specimens upon which this study is based. I would like to thank Dr. Charles D. Michener for his help in reading and editing this paper, and Dr. Jack L. Boese for his encouragement, for his help in checking the key, and for reading the manuscript.

Most larvae examined were obtained from field studies supported by Grant GB-7045X from the National Science Foundation to G. W. Byers.

MATERIALS AND METHODS

Larval specimens were preserved in 70% alcohol. For examination each larva was placed in a small dish half-filled with paraffin, held in place by a thread tied between two pins, and covered with 70%

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alcohol. Drawings were made with the aid of an ocular grid.

Setal measurements were taken with an ocular micrometer. Broken tips were so recorded. The actual length of the body was measured regardless of how much the body curved, although most larvae were almost fully outstretched.

The species examined were *P. acuta, P. anomala, P. banksi, P. carolinensis, P. claripennis, P. flexa* (?), *P. helena, P. latipennis, P. lugubris, P. mirabilis, P. nebulosa, P. nuptialis,* and *P. subulifera.* Except for *P. lugubris,* 4 to 11 larvae of each species were examined.

The system of nomenclature of the setae in this paper is that of Yie (1951), which is based on Fracker's (1916) system for lepidopterous larvae. Only the setae and pinacula on the left side of the larva will be described. Unless otherwise stated, this description applies to the right side also.

MORPHOLOGY

General morphology of larva. Panorpa larvae are eruciform, have three-segmented antennae, and chewing mouthparts. The abdomen has ten segments, the first eight with small, subconical prolegs that have short hairs on the tips. The body is sparsely covered with setae.

Larva. The first instar larva has an annulated seta on each side of the median dorsal line on the first nine abdominal terga. The tenth abdominal tergum has only a single median seta. The head is large in comparison to the slender body, and the legs are relatively long. Also, the antennae are relatively much thicker than in the full-grown larva (Brauer, 1863). The length of the body does not begin to increase greatly until after the first molt (Byers, 1963).

Differentiation of instars. During the second, third, and fourth stadia, the larva grows larger and becomes darker, and the segmentation becomes more evident. The antennae have progressively shorter flagellar segments in comparison to the scape and pedicel, but there is no great change in their morphology. The second, third, and fourth instars are similar to each other, except with each molt there is a decrease in the width of the head and the size of the legs in proportion to the body as a whole, and an increase in the sclerotization of the tergal plates and pronotal shield (Byers, 1963). On the first seven abdominal segments, the annulated setae are vestigial after the first larval stadium; however, those on the eighth to tenth abdominal segments remain during all stadia.

The other instars can be distinguished mainly by the relative sizes of the body and head capsules, and variation in the size of the annulated setae. Gassner (1963) differentiated fourth from third instar larvae by the presence in the former of sclerotized pedicels between the annulated setae and by their subconical bases on the eighth to tenth abdominal segments.

Number of larval molts. Based upon the ratio of the head widths between first and second instars, Felt (1896), applying Dyar's (1890) rule to calculate the width of the head expected in succeeding instars, deduced that there were seven stages. Miyaké (1912) applied Dyar's rule to Japanese species and also calculated that there were seven stages. However, Yie (1951) observed that *Panorpa* larvae have four stages. He examined the width of the head and computed the ratios according to Dyar's rule, confirming his observations of four stages. Also, Byers (1963) recovered cast skins at each molt, showing the existence of four instars. He computed the increase in both length and width of the head capsule to be an average factor of 1.46 with each molt.

Spiracles. A *Panorpa* larva has nine pairs of spiracles, one pair on the posterior

part of the dorsal shield of the prothorax, and the other eight pairs located on separate, rounded pinacula on the first eight abdominal segments. The spiracles are of the primitive type, being surrounded by sclerites called peritremes (Applegarth, 1939). There is a darkened portion in the center of each spiracle with small oval apertures arranged radially around it. Under the apertures is a common cavity, the spiracular atrium.

The prothoracic spiracles are larger and have more apertures than the abdominal spiracles. The number of apertures in the abdominal spiracles decreases from the anterior to the posterior end of the body. The number of spiracular apertures also varies among species. *P. acuta* specimens have 36-40 apertures in the prothoracic spiracle of the fourth instar; *P. anomala,* 34-36; *P. banksi,* 36-42; *P. carolinensis,* 40-44; *P. claripennis,* 38-42; *P. flexa* (?) 36-40; *P. helena,* 36-40; *P. latipennis,* 42-46; *P. mirabilis,* 36-40; *P. nebulosa,* 36-40; *P. nuptialis,* 48-52; *P. subulifera,* 36-40; and *P. lugubris,* 52 apertures.

The main change in the spiracles from one instar to the next is an increase in the number of apertures. The septa between them increase in size and become more readily visible, while the apertures themselves become smaller. The entire spiracle becomes darker, and the middle portion becomes larger and eventually either T-shaped or like an irregular ellipse.

Head. The head is dark reddish brown when the specimen is preserved in 70% alcohol. It is large in comparison to the body. The dorsal and lateral surfaces are curved and the ventral surface is flattened. The posterior part of the head is rounded and attached to a membranous neck. The head has 13 sets of setae.

Laterally on the head there are four setae, S_1, S_2, S_3, and S_4 (Fig. 28). Seta S_1 is on the anterior end of the gena near the ventral articulation of the mandible and slightly anterior to it. S_2 arises near the ocular suture on the ventral side of the compound eye. S_3 is ventral to S_2 and posterior to S_1. S_4 is near the middle of the gena, dorsal to S_3 and posterior to the compound eye. S_1 is 1.5-2 times as long as S_4. Although there is some variation among species and specimens, S_1 is usually the longest with S_2, S_3, and S_4 being progressively shorter.

On the dorsal surface of the head are nine sets of prominent setae and various sutures (Fig. 24) which include set SO, a pair of setae near the ocular suture and dorsal to the compound eye; set SI, two pairs of setae on the anterior border of the labrum with the outer ones twice as long as the inner ones; set SII, four setae near the median part of the clypeus; set SIII, two setae near the epistomal suture; set SIV, two setae on the frons near the frontal suture located midway between the epistomal suture and the anterior end of the coronal suture; set SV, two setae on the upper part of the genae; and set SVI, two setae between the vertex and the genae. Set SVII is a pair of setae located between the vertex and the post-vertex on the occipital suture on the upper posterior portion of the genae. Set SVIII is a small pair of setae located lateral to set SVII. The relative lengths of setae SII through SVIII vary from species to species and also within species.

Eye. The eyes consist of roughly hexagonal facets varying in number from 24 to 30 per eye (Fig. 22). Each eye is surrounded by an ocular suture. The number of facets listed for the eyes by Byers is 25 or more in *P. nuptialis.* Miyaké recorded 28 in *P. klugi* and Felt counted about 20 in *P. debilis* (as *rufescens*). The color of the eyes varies in preserved specimens from clear white to purple to purple-black. It is nearly black in living larvae.

Antenna. The antennae are inserted in a socket close to and anterior to the eye

on the dorso-lateral surface of the head. Each consists of a scape, pedicel, and flagellum (Fig. 23). The scape is short with a broad base and appears subdivided by a sclerotized band around the middle. The pedicel is longer than the scape and bulbous at the distal end. The flagellum is a single slender segment, its length approximately equal to the basal diameter of the pedicel. The width of the base of the pedicel is less than the width of the base of the scape. The length of the pedicel is two times or more the length of the flagellum.

Mouthparts. The prognathous mouthparts are the biting-chewing type. The mandibles, which project from the sides of the head near the antennae, are piceous, heavily sclerotized, large in proportion to the other mouthparts, and triangular with an inwardly curved apex (Fig. 28). They are reddish brown when preserved in 70% alcohol. The mandible bears three setae, one apical, S_a, one median, S_m, and the third basal, S_b. Setae S_a and S_b are approximately equal and shorter than S_m.

The labrum is trapezoidal and projects forward above the mandibles, forming the dorsal (anterior) wall of the pre-oral cavity. Near its postero-lateral corners are two small sclerites, tormae, which extend into the clypeus. On the anterior border of the labrum are rows of dense spicules and two pairs of setae, set SI. Between these setae there are, depending on the species, either two or three pairs of very minute setae. Rigidly connected to the inner surface of the labrum is a small, short, median sclerite obtuse at its posterior end (Yie, 1951).

The basal part of the maxilla or stipes is a band-like sclerite set at a 45-degree angle to the longitudinal axis of the body. There are two condyles on the posterior border of this sclerite. This basal sclerite bears an inner membranous lacinia, and an outer strongly sclerotized galea bears two large setae and two minute setae. A four-segmented palpus arises lateral to the galea. It has three subequal, cylindrical segments, the last segment cylindrical with rounded apex and twice as long as the basal segment (Yie, 1951).

The labium has three-segmented labial palpi whose bases are united and attached to the median ventral anterior margin of the postmentum. The postmentum forms part of the ventral wall of the head. It is divided by a longitudinal suture but lacks the usual transverse suture. The apical segment of the palpus is as long as the combined lengths of the other two. It also bears six setae. The basal segment is covered with hair-like growths (Yie, 1951).

Thorax. In specimens preserved in 70% alcohol, the thorax is pale yellow and gray with a yellowish brown, sclerotized dorsal shield on each segment. The prothorax (Fig. 29) has a prominent rectangular dorsal shield which bears eight setae and has a large spiracle near each postero-lateral corner. Of these setae, four are on the anterior margin: α (anterior dorsal), γ (anterior latero-dorsal), ϵ (upper lateral), η (minute lower anterior lateral); three are on the posterior margin: β (posterior dorsal), ρ (upper posterior lateral), ρ' (second upper posterior lateral); and one is on the dorsal margin: δ (posterior latero-dorsal). In addition to the setae on the dorsal shield, there are eight others on the prothorax. Seta κ (prominent, lower anterior lateral) is on a rounded pinaculum just below the shield. On the other rounded pinaculum are four setae: υ (anterior latero-ventral), υ' (second latero-ventral), π (posterior latero-ventral), and π' (second posterior latero-ventral). Setae υ' and π' are approximately the same length, though υ' may be slightly shorter, and both are shorter than υ or π. Three setae are on the prothoracic leg: τ (upper anterior ventral), ω (lower anterior ventral), and σ (posterior ventral). Just anterior to

the antero-lateral corner of the prothorax is a crescent-shaped sclerite (not illustrated) with two or three small, unnamed setae.

The mesothorax and the metathorax are similar in structure. As seen in Figure 4, each has an irregular elliptical dorsal shield with five setae, α, δ, ρ, ρ', and β. Seta ρ is the longest and α is minute. Setae δ, ρ, and β are grouped closely together and are closer to each other than to ρ'. There are three lateral rounded pinacula each with two setae (υ and υ', ϵ and ϵ', η and κ) below which are two pinacula, one with setae υ and υ' and the other with π and π'. The prothoracic pinaculum with these setae is not divided into two smaller pinacula, but the relative lengths of υ, υ', π, and π' are the same as on the prothorax. The remaining setae on the mesothorax and metathorax are the same as those on the prothorax, with the addition of υ' (second anterior latero-dorsal) and ϵ' (second upper anterior lateral). The middle lateral pinaculum with ϵ and ϵ' has a tiny seta located just anterior to it in most species. It is called seta 3 by Mampe and Neunzig (1965) but is not named by Yie (1951). The distance between this extra seta and ϵ' is equal to or greater than the distance between ϵ and ϵ'.

Abdomen. The first seven abdominal segments are similar in structure. As seen in Figure 2, each has a small dorsal shield and five setae, ρ, ρ', β, δ, and α, and a small subconical process. Seta δ is located closer to β than to α, and ρ' is located closer to ρ than to α. The spiracle is located on a separate pinaculum. Two additional setae are present: θ (lower posterior lateral) on the pinaculum with κ and η, and υ'' on the pinaculum with υ and υ'. Seta κ is long, slender, and aciculate, compared to short, spatulate setae η and θ, which are equidistant from κ on either side. There are only two prominent setae on each proleg, τ and ω, but there are many microscopic setae on its tip. Setae γ, γ', and ϵ are on a rounded pinaculum near the dorsal shield. Seta ϵ' (second upper anterior lateral) is not present. Setae γ, γ', and ϵ are equidistant and in most specimens form a triangle with γ' as the most anterior point, γ, the most posterior, and ϵ the lower point. Seta γ is longer than ϵ which is longer than γ'.

The eighth abdominal segment (Fig. 5) has an irregularly shaped dorsal shield with three setae, γ, δ, and α. In a few specimens of various species seta ρ is present. There is a pair of median subconical processes (each with an annulated seta) on the tergum. Setae β, ρ', γ', and ϵ are not present, but the setae and pinacula posterior and ventral to the spiracular pinaculum are the same as on the first seven abdominal segments.

The dorsal shield and subconical process of the ninth abdominal segment (Fig. 18) are similar to those of the eighth. There are no spiracles or prolegs on this segment, and setae θ, π', υ', and υ'' are absent. Seta ω is on a small pinaculum on the ventral side of the segment. Seta ω' (second lower anterior ventral) occurs on the pinaculum with ω.

The dorsal shield of the tenth abdominal segment (Fig. 27) has only a single median subconical process. The shield has ventro-lateral finger-like projections with a small seta at the tip of each. The dorsal part of the shield extends into a posterior rectangular area with two setae. As on the ninth abdominal segment, there are no spiracles or prolegs. Setae κ, η, and θ are absent, but seta ω'' occurs on the pinaculum with ω and ω'.

DESCRIPTIONS OF SPECIES

Panorpa acuta Carpenter, 1931

Eight fourth instar larvae examined (reared from adults collected in Mountain Lake area, Giles County, Virginia, G. W.

Byers rearing lot no. 133). Fourth instar larva 10.5—12 mm long. On lateral surface of head S_1 longest seta and in some specimens equal to S_2 or only slightly longer. Both setae longer than S_3 and S_4. On dorsal surface SVII twice as long as SVIII and in most specimens outside pair in set SI twice as long as inside pair.

Seta γ on anterior margin of prothoracic shield slender, somewhat pointed, equal in width throughout to tip. Several extra punctures near α, γ, and ϵ on anterior margin. Seta η represented by a setiferous plate or puncture, not in a straight line with α, γ, and ϵ, but located in mid-ventral region of shield near spiracle. On posterior margin of shield, ρ' not in a straight line with β and ρ, but slightly anterior to them. Seta ρ three times length of ρ' and two times length of β. Length of rectangular pinaculum with π and υ 2-2.5 times its width. Seta υ about three-fourths length of π, and υ' three-fourths of π'.

Seta ρ on dorsal shield of metathorax two times or more length of β (Fig. 1). Seta β slightly longer than δ and ρ'. In most specimens δ and ρ' equal in length. Seta ρ' located closer to ρ than to α. An extra seta located near rounded pinaculum with ϵ and ϵ' and in a straight line with them. Seta κ three times or more length of η and γ, four times or more length of γ'. Pinaculum with υ and υ' almost rectangular, but pinaculum with π and π' with a ventral extension from its anterior portion appears L-shaped. Seta υ less than three-fourths length of π.

On each of first seven abdominal segments (Fig. 2) setae ρ' and β approximately equal and both shorter than ρ and longer than δ. Seta σ twice as long as τ and ω which are equal.

Two setae, γ and δ, on dorsal shield of eighth abdominal segment (Fig. 3). Seta ρ and α absent. Setae γ and δ equal in length and each less than half width of base of subconical process. Seta π two times or more length of π'.

On dorsal shield of ninth abdominal segment three setae, γ, δ, and ρ, approximately equal in length and each less than half width of base of subconical process. Seta α may be present in some specimens. Seta π minute. Setae ω and ω' on a single pinaculum ventral to σ.

On dorsal shield of tenth abdominal segment three setae, γ, δ, and ρ, each less than half width of base of subconical process. Seta γ slightly longer than ρ. Seta α absent. Setae ω, ω', and ω'' located on a single ventral pinaculum. In a few specimens, ω'' may be absent.

Panorpa anomala Carpenter, 1931

Six fourth instar larvae examined (reared from adults collected in Baldwin Woods, Douglas County, Kansas, G. W. Byers rearing lot no. 156). Fourth instar larva 10-12 mm long. Four setae on lateral surface of head with S_1 longest and length of other three setae varying individually. Outside pair of setae of set SI two or more times length of inside pair. Seta SVII 1.5-2 times length of SVIII.

Seta γ on anterior margin of prothoracic shield slender, pointed, and either equal in width throughout or broader at base than at tip. Seta η represented by a setiferous plate or puncture and located midway between spiracle and anterior margin of shield. Several extra punctures located on anterior margin of shield. On posterior margin of prothoracic shield ρ' not in a straight line with β and ρ. Seta ρ 1.5-2 times length of β and 3-4 times length of ρ'. Length of rectangular pinaculum with π and υ three times its width. Seta υ three-fourths length of π, and υ' equal to π'.

Seta ρ on dorsal shield of metathorax about two times as long as β (Fig. 4). Seta β 1.5-2 times length of δ and ρ' which are equal. Seta ρ' equidistant from ρ and

α. An extra seta located near the pinaculum with ϵ and ϵ', and almost in a straight line with them. Seta κ three times or more length of η, and γ four times or more length of γ'. Pinaculum with π and π' almost rectangular and without lobe-like extension. Seta π almost 1.5 times length of υ.

On each of first seven abdominal segments seta ρ longer than β which is longer than ρ' and δ which are almost equal. In most specimens ρ' three-fourths length of β, but in two specimens ρ' and β equal. Seta σ twice as long as τ and ω which are equal.

Three setae, γ, δ, and α, on dorsal shield of eighth abdominal segment (Fig. 5). In a few specimens ρ may be present. Setae γ and δ equal in length and each less than width of base of subconical process. Seta π two times or more length of π'.

Four setae, γ, δ, ρ, and α, on dorsal shield of ninth abdominal segment (Fig. 6). Setae γ, δ, and ρ approximately same length and each less than half width of base of subconical process. In some specimens α may be absent. Seta π absent. Setae ω and ω' almost equal in length and located on two separate ventral pinacula. In a few specimens ω'' may be present.

On dorsal shield of tenth abdominal segment are three setae, γ, δ, and ρ, equal in length and each less than half width of base of subconical process. Seta α absent. Setae ω, ω', and ω'' located on a single ventral pinaculum. In a few specimens ω'' may be absent.

Panorpa banksi Hine, 1901

Five fourth instar larvae examined (reared by A. R. Thornhill from adults collected in Washtenaw County, Michigan). Fourth instar larva 12-14 mm long. On the lateral surface of the head S_1 longest seta and setae S_2 and S_3 both longer than S_4. On dorsal surface SVII almost twice as long as SVIII.

Seta γ on anterior margin of prothoracic shield slender, somewhat pointed, and equal in width throughout to tip. One or several extra setal punctures near α, γ, and ϵ on anterior margin of dorsal shield. Seta η usually represented by a setiferous plate or puncture not in a straight line with α, γ, and ϵ, but in midventral region of shield near spiracle. On posterior margin of shield in two specimens ρ' in a straight line with β and ρ, and in three specimens ρ' not in a straight line, but slightly anterior to β and ρ. Seta ρ two times length of β which is longer than ρ'. Length of rectangular pinaculum with π and ν 3.5-4 times its width. Seta ν about three-fourths length of π. Setae ν' and π' almost equal in length.

Seta ρ on dorsal shield of metathorax 2.5-3 times length of β. Seta β longer than δ and ρ' which are almost equal in length. Seta ρ' equidistant from ρ and α. In two specimens an extra seta located near rounded pinaculum with ϵ and ϵ'. In three specimens both ϵ' and extra seta absent. Seta γ longer than κ and both four or more times longer than η and γ' which are approximately equal in length. Pinaculum with ν and ν' and pinaculum with π and π' both almost rectangular. Relative lengths of ν, π, ν', and π' are same as on prothorax.

On dorsal shield of first seven abdominal segments δ and ρ' approximately equal and shorter than β. Seta ρ longest and 1.5-2.5 times length of β. Seta α absent. Seta σ 1.5-2.5 times length of τ and ω which are equal.

Two setae, γ and δ, on dorsal shield of eighth abdominal segment. Seta ρ absent. Seta α absent in two specimens and present in three specimens. Setae γ and δ equal in length and each half or less width of base of subconical process. Seta π 2.5 times or more length of π'.

On dorsal shield of ninth abdominal

segment three setae, γ, δ, and ρ, approximately equal in length and each less than half width of base of subconical process. Setae α, π, and ω' absent. Setae ω and σ almost equal in length and located on two small circular pinacula.

On dorsal shield of tenth abdominal segment are three setae, γ, δ, and ρ, about equal in length and each half or less width of base of subconical process. Seta α absent. Three setae, ω, ω', and ω'', on a pinaculum ventral to σ. Seta ω'' absent in one specimen.

Panorpa carolinensis Banks, 1905

Five fourth instar larvae examined (reared from adults collected in Great Smoky Mountains National Park, elevation 5600 feet, Swain County, North Carolina, G. W. Byers rearing lot no. 158). Fourth instar larva 12-12.5 mm long. On lateral surface of head S_1 longest seta, about twice as long as shortest seta, S_4. On dorsal surface, seta SO longest, slightly longer than SIV, SV, and SVI which are equal in length. SVII two times length of SVIII.

Seta γ on prothoracic shield pointed and more slender at distal end than at base. Seta η represented by a setiferous plate or puncture in mid-ventral region near spiracle. Several extra punctures on anterior margin of shield. On posterior margin of shield ρ' not in straight line with β and ρ. Seta ρ two times or more length of β. Length of rectangular pinaculum with setae π and υ three times its width. Seta υ half to three-fourths length of π. Setae υ' and π' approximately equal.

Seta ρ on dorsal shield of metathorax two times or more length of β (Fig. 7). Setae δ and ρ' equal and half length of β. Seta ρ' equidistant from ρ and α. An extra seta located by pinaculum with ϵ and ϵ' in some specimens and often not in a straight line with them. Seta κ four times or more length of η, and γ five times or more length of γ'. Relative lengths of π, π', υ, and υ' same as on prothorax. Anterior part of pinaculum with π and π' extended into lobe.

On dorsal shield of each of first seven abdominal segments (Fig. 8) seta ρ longer than β which is 1.5-2 times length of ρ' and δ which are approximately equal. Seta α absent. Seta τ and ω equal and three-fourths length of σ.

Two setae, γ and δ, on dorsal shield of eighth abdominal segment (Fig. 9). In a few specimens ρ may be present. Setae γ and δ equal and each less than half width of base of subconical process. Seta π two times or more length of π'.

On dorsal shield of ninth abdominal segment (Fig. 10) three setae, γ, δ, and ρ, equal in length and each half width of base of subconical process. Seta α absent. Seta π either absent or minute. Seta ω and ω' approximately equal, on a single ventral pinaculum.

On dorsal shield of tenth abdominal segment three setae, γ, δ, and ρ, equal in length and each less than half width of base of subconical process. Seta α absent. Two setae, ω and ω', on a single ventral pinaculum. Rarely, ω'' also present.

Panorpa claripennis Hine, 1901

Four fourth instar larvae examined (reared by A. R. Thornhill from adults collected in Washtenaw County, Michigan). Fourth instar larva 12.0-14.5 mm long. On the lateral surface of the head S_1 longest seta, and S_2 and S_3 both longer than S_4. On dorsal surface SVII longer than SVIII and S0 longest seta.

Seta γ on anterior margin of prothoracic shield slender, somewhat pointed, and equal in width throughout to its tip. In most specimens one or several extra setal punctures near α, γ, and ϵ on anterior margin. Seta η usually represented by a setiferous plate or puncture not in a straight line with α, γ, and ϵ, but in

mid-ventral region of shield near spiracle. On posterior margin of shield ρ' not in a straight line with β and ρ. Seta ρ 1.5-2 times length of β which is slightly longer than ρ'. Length of rectangular pinaculum with π and ν 3.5-4 times its width. Seta ν one-half to three-fourths length of π, and ν' and π' almost equal in length. Seta π' may be slightly longer.

Seta ρ on dorsal shield of metathorax more than two times length of β. Seta δ and ρ' almost equal in length and shorter than β. Seta ϵ' absent. Seta κ 3-4 times length of η, and γ four times or more length of γ'. Seta γ one-half to three-fourths length of π. Seta π' slightly longer than ν'. Pinaculum with π and π' not rectangular but extended ventrally into a bluntly pointed lobe.

On dorsal shield of first seven abdominal segments δ, ρ', and β approximately equal in length and each is one-half or less length of ρ. Seta α is absent. Seta σ two times length of τ and ω which are equal.

Two setae, γ and δ, on dorsal shield of eighth abdominal segment. Seta ρ absent. Seta α absent in three specimens and present in one. Setae γ and δ equal in length and each three-fourths or less width of base of subconical process. Seta π 2-3 times length of π'.

Three setae, γ, δ, and ρ, on dorsal shield of ninth abdominal segment. Seta α absent. Setae γ, δ, and ρ equal in length and each one-half width of base of subconical process. An extra seta on dorsal shield near γ and ρ. Seta π absent. Seta ω and ω' on a single ventral pinaculum. Seta ω' minute and much shorter than ω.

Three setae, γ, δ, and ρ, on dorsal shield of tenth abdominal segment. Seta α absent. Each seta, γ, δ, and ρ, one-half or less width of base of subconical process. Setae ω and ω' equal in length and located on a single ventral pinaculum.

Panorpa flexa (?) Carpenter, 1935

Nine fourth instar larvae examined (collected in pit traps on Clingmans Dome, elevation 6000 feet, Great Smoky Mountains National Park, Tennessee, by Thomas Hlavac). The specimens were tentatively identified as *P. flexa* because they were collected in a locality that only two species of *Panorpa* (*carolinensis* and *flexa*) are known to inhabit. The larvae differ consistently from those of *carolinensis* and are thus assumed to be *P. flexa*. Also these larvae are very similar to those of *P. nebulosa*, nearest relative of *flexa*.

Fourth instar larvae 11-12 mm long. On lateral surface of head S_1 slightly longer than S_2 and both longer than S_3 and S_4 which are approximately equal. On dorsal surface of head SVII twice as long as SVIII, and outside pair of setae in set SI twice as long as inside pair.

Seta γ on prothoracic shield either equal in width throughout or slightly broader at distal end than at base. On posterior margin of shield ρ' not in a straight line with β and ρ. Seta ρ 2-2.5 times length of β and 3-4 times length of ρ'. Seta η represented by puncture located in mid-ventral region of shield near spiracle. Rarely seta η located on anterior margin of shield. Length of rectangular pinaculum with π and υ 2.5 times its width. Seta υ two-thirds length of π.

Seta ρ on dorsal shield of metathorax (Fig. 11) 2-2.5 times length of β. Seta β 1.5-2 times length of ρ. Usually ρ' equal to δ, but in a few specimens ρ' slightly longer. Seta ρ' closer to ρ than to α. Rarely an extra seta located adjacent to and above pinaculum with ϵ and ϵ' and in a straight line with them. Seta κ four times length of η, and γ 3-4 times length of γ'. Pinaculum with π and π' extends ventrally into a bluntly pointed lobe which almost forms a triangle.

On dorsal shield of each of first seven abdominal segments ρ the longest seta.

Seta β slightly longer than ρ' which is slightly longer than δ. Seta σ 1.5-2 times length of τ and ω which are equal.

Two setae, γ and δ, on dorsal shield of eighth abdominal segment. Seta ρ and α absent, or α rarely present. Setae γ and δ each less than half width of base of subconical process. Seta π' half length of π.

Three setae, γ, δ, and ρ, on dorsal shield of ninth abdominal segment (Fig. 12). Seta α absent. Setae γ, δ, and ρ equal in length and each less than half width of base of subconical process. An extra seta on dorsal shield near γ and ρ. Setae ω and ω' on a single ventral pinaculum, ω' minute.

Three setae, γ, δ, and ρ, on dorsal shield of tenth abdominal segment. Seta α absent. Each seta, γ, δ, and ρ, less than half width of base of subconical process. Three setae, ω, ω', and ω'', located on a pinaculum ventral to σ.

Panorpa helena Byers, 1962

Nine fourth instar larvae examined (reared from adults collected in Baldwin Woods, 15 miles southeast of Lawrence, Douglas County, Kansas, G. W. Byers rearing lot no. 157). Fourth instar larva 11-13.5 mm long. On lateral surface of head S_1 longest seta and S_1 shortest. Outside pair of setae in set SI twice as long as inside pair. Seta SVII almost as long as SVIII.

Seta γ on anterior margin of prothoracic shield somewhat pointed and equal in width throughout. Seta η represented by a setiferous plate or puncture and located midway between anterior margin of shield and spiracle. Seta ρ' not in a straight line with β and ρ. Seta ρ 1.5-2 times length of β and three times or more length of ρ'. Length of rectangular pinaculum with π and υ three times or more its width. Seta υ half to three-fourths length of π which is three times or more length of π'.

On dorsal shield of metathorax seta β three-fourths length of ρ and 2-3 times length of δ and ρ' which are equal. Seta ρ' closer to ρ than to α. An extra seta located adjacent to and slightly above pinaculum with ϵ and ϵ' and in a straight line with them. Seta κ four times or more length of η, and γ about four times length of γ'. Relative lengths of π and υ same as on prothorax. Pinaculum with π and π' rectangular.

On each side of first seven abdominal segments, ρ longer than β which is 1.5-2 times length of ρ' and δ which are equal. Seta σ two times as long as τ and ω which are equal.

Three setae, γ, δ, and α, on dorsal shield of eighth abdominal segment. Setae γ and δ equal and each shorter than width of base of subconical process. In two specimens an extra seta near γ on posterior margin of shield. Seta π two times or more length of π'.

Four setae, γ, δ, ρ, and α, on dorsal shield of ninth abdominal segment (Fig. 18). In a few specimens α may be absent. Setae γ, δ, and ρ approximately equal and half width of base of subconical process. Seta π absent or minute. Setae ω and ω' located on a single ventral pinaculum. Seta ω' minute, absent in some specimens.

Three setae, γ, δ, and ρ, on dorsal shield of tenth abdominal segment. Seta α absent. Each seta, γ, δ, and ρ, shorter than width of base of subconical process. Two, ω and ω', to four, ω, ω', ω'', and ω''', setae on single pinaculum ventral to σ.

Panorpa latipennis Hine, 1901

Ten fourth instar larvae examined (reared from adults collected at Wind Rock near Mountain Lake Biological Station, Giles County, Virginia, G. W. Byers rearing lot no. 130). Fourth instar larva 15-16 mm long. On lateral surface of head S_1 longest seta and S_1 shortest. In one specimen S_3 shortest. Seta S0 longest seta on head. Setae SIV and SV approximately

equal. Seta SVII two times or more length of SVIII.

Seta γ on anterior margin of prothoracic shield (Fig. 15) equal in width throughout in some specimens, but in others more slender at its base. Seta ρ' not in a straight line with β and ρ. Seta ρ two times or more length of ρ'. Seta η represented by a puncture in mid-ventral region of shield near spiracle. Several additional punctures on anterior margin of shield. Length of pinaculum with π and υ three times its width. Seta υ three-fourths length of π, and υ' slightly shorter than π'.

Seta ρ on dorsal shield of metathorax more than two times length of β which is 1.5 times length of ρ'. Seta ρ' slightly longer than δ, and ρ three times length of δ. Seta ρ' closer to ρ than to α. An extra seta near pinaculum with ϵ and ϵ' and not in a straight line with them. Seta κ 3-4 times length of η, and γ 3-4 times length of γ'. Relative lengths of π and υ same as on prothorax. Setae υ' and π' approximately equal, and π four times length of π'. Pinaculum with π and π' not rectangular, extended ventrally into a bluntly pointed lobe, which in some specimens almost forms a triangle.

On dorsal shield of each of first seven abdominal segments seta ρ longer than β. In some specimens β equal to ρ' and in others 1.5-2 times its length. Setae ρ' and δ approximately equal. Seta γ three times length of ϵ, and γ' minute. Setae τ and ω 1.5-1.75 length of σ.

Three setae, γ, δ, and α, on dorsal shield of eighth abdominal segment (Fig. 16). Seta ρ absent. Each seta, γ and δ, not as long as width of base of subconical process. Seta π 1.5-2.5 times length of π'.

On dorsal shield of ninth abdominal segment (Fig. 17) three setae, γ, δ, andρ, equal in length and each less than half width of base of subconical process. Seta α absent. Seta π either absent or minute. A minute extra seta (or setal puncture if seta is missing) on posterior margin of shield near γ and ρ. Setae ω and ω' on a single ventral pinaculum, ω five times or more length of ω'.

On dorsal shield of tenth abdominal segment three setae, γ, δ, and ρ, each less than half width of base of subconical process. Seta γ slightly longer than ρ. Seta α absent. Setae ω, ω' and ω'' on a single ventral pinaculum. In a few specimens ω'' absent.

Panorpa lugubris Swederus, 1787

Two fourth instar larvae examined (specimens provided by Dr. Herbert H. Neunzig, North Carolina State University, Raleigh, North Carolina). Fourth instar larva about 19 mm long. On lateral surface of head S_1 longest seta and about 1.5 times length of shortest seta, S_4. Seta S_3 longer than S_2 which is longer than S_4. Outside pair of setae in set SI two times or more length of inside pair. SVII two times or more length of SVIII. Seta S0 longest seta on head.

Seta γ on anterior margin of prothoracic shield (Fig. 13) longest seta and slightly longer than α and ϵ which are about equal in length. Seta γ somewhat pointed and either equal in width throughout or broader at basal end than at apex. Seta η represented by a puncture in a straight line with α, γ, and ϵ on anterior margin of shield. On posterior margin of shield ρ in a straight line with ρ and β. Seta ρ 1.5 times length of β and two times or more length of ρ'. In one specimen π slightly longer than υ and in the other υ slightly longer than π.

On dorsal shield of metathorax ρ the longest seta. In one specimen ρ' equidistant from ρ and α and in the other slightly closer to ρ. An extra seta near pinaculum with ϵ and ϵ' and in a straight line with them. Seta κ almost twice as long as η, and γ more than two times as long as γ'. Pinaculum with π and π' rectangular.

On each of first seven abdominal segments ρ the longest seta and longer than β which is either slightly longer than or equal to ρ' and δ which are equal. Seta σ 1.5-2 times as long as τ and ω which are almost equal.

Three setae, γ, δ, and α, on dorsal shield of eighth abdominal segment. Seta ρ absent. Setae γ and δ equal and each longer than width of base of subconical process.

Four setae, γ, δ, ρ, and α, on dorsal shield of ninth abdominal segment. Setae γ, δ, and ρ equal in length and each slightly longer than width of base of subconical process. A minute extra seta located between γ and ρ on posterior margin of shield. Seta π minute. Setae ω and ω' equal, on two small separate ventral pinacula.

On dorsal shield of tenth abdominal segment (Fig. 14) each setae, γ, δ, and ρ, longer than width of base of subconical process. Seta γ slightly longer than ρ. Seta α either minute or absent. In one specimen four setae, ω, ω', ω'', and ω''', on a single ventral pinaculum, but in other specimen ω''' absent.

Panorpa mirabilis Carpenter, 1931

Ten fourth instar larvae examined (reared by A. R. Thornhill from adults collected in Washtenaw County, Michigan). Fourth instar larva 13.5-15.5 mm long. On the lateral surface of the head S_1 longest seta, S_2, second, S_3, third, and S_4 shortest seta. On the dorsal surface of the head SVII is 1.5-2.5 times length of SVIII.

Seta γ on anterior margin of dorsal shield of prothorax slender, somewhat pointed, and equal in width throughout to tip. In some specimens one or several extra setal punctures near α, γ, and ϵ on anterior margin of shield. Seta η represented by a setiferous plate or puncture not in a straight line with α, γ, and ϵ, but in the mid-ventral region of the dorsal shield near spiracle. On posterior margin of shield in six specimens ρ' in a straight line with β and ρ, and in four specimens ρ' not in a straight line, but slightly anterior to β and ρ. Seta ρ 1.5-2.5 times length of β which is longer than ρ'. Length of rectangular pinaculum with π and ν 3.5-4 times its width. Seta ν about three-fourths length of π. Seta π' equal to or slightly longer than ν'.

Seta ρ on dorsal shield of metathorax two times length of β. Setae δ and ρ' almost equal in length and shorter than β. Seta ρ' equidistant from ρ and α. In some specimens ϵ' is absent. Seta κ 2.5 times or more length of η, and ν four times or more length of γ'. Seta ν one-half to three-fourths length of ν'. Seta π' slightly longer than ν'. Pinaculum with π and π' rectangular.

On dorsal shield of first seven abdominal segments ρ' and δ about equal in length and slightly shorter than β. All three setae one-half or less length of ρ. Seta α present but minute in length in five specimens and absent in five specimens. Seta σ 1.5-2 times length of τ and ω which are equal.

Two setae, γ and δ, on dorsal shield of eighth abdominal segment. Seta ρ absent. Seta α absent in eight specimens and present as a minute seta in two specimens. Seta γ and δ equal in length and each shorter than width of base of subconical process. Seta π 2-4 times length of π'.

Three setae, γ, δ, and ρ, on dorsal shield of ninth abdominal segment. Setae α, π, and ω' absent. Setae γ, δ, and ρ equal in length and one-half or less width of base of subconical process. Setae ω and σ equal in length and located on two small circular pinacula.

On dorsal shield of tenth abdominal segment, three setae, γ, δ, and ρ, equal in length and each seta half or less width of base of subconical process. Seta α ab-

sent. Setae ω and ω' equal in length and located on a single ventral pinaculum. Seta ω'' absent.

Panorpa nebulosa Westwood, 1846

Nine fourth instar larvae examined (reared from adults collected in Mountain Lake area, elevation 4100 feet, Giles County, Virginia, G. W. Byers rearing lot no. 131). Fourth instar larva 11-12 mm long. On lateral surface of head S_1 and S_2 equal in length and longer than S_3 and S_4. S_4 the shortest seta. On dorsal surface of head SVII twice as long as SVIII. Outside pair of setae of set SI two times or more length of inside pair.

On prothoracic shield set γ somewhat pointed and equal in width or slightly wider at apical than at basal end. On posterior margin of shield ρ' not in a straight line with β and ρ. Seta ρ two times length of β and much longer than ρ' which is minute. Seta η represented by a puncture located in mid-ventral region of shield near spiracle. Several extra punctures present on anterior margin of shield. Length of rectangular pinaculum with π and υ 2.5 times width. Seta υ less than three-fourths length of π.

Seta ρ on dorsal shield of metathorax (Fig. 19) two times or more length of β. Seta β 1.5-2 times length of ρ' which is slightly longer than δ. Seta ρ' almost equidistant from α and ρ. No extra seta near pinaculum with ϵ and ϵ'. Seta κ four times or more length of η, and γ four times or more length of γ'. Relative lengths of υ, υ', π, and π' same as on prothorax. Pinaculum with π and π' extends ventrally into bluntly pointed lobe almost forming a triangle.

On dorsal shield of each of first seven abdominal segments (Fig. 20) seta ρ longer than β which is longer than ρ' and δ. In some specimens ρ' longer than δ, but in others ρ' and δ equal in length. Seta σ almost twice as long as τ and ω which are equal.

Three setae, γ, δ, and α, on dorsal shield of eighth abdominal segment (Fig. 21). Seta ρ absent. In some specimens α absent also. Each seta, γ and δ, less than half width of base of subconical process. Seta π more than two times length of π'.

Three setae, γ, δ, and ρ, on dorsal shield of ninth abdominal segment. Seta α absent. Seta π minute or absent. Setae γ, δ, and ρ approximately same length and each less than half width of base of subconical process. Setae ω and ω' on single ventral pinaculum. Seta ω' minute.

Three setae, γ, δ, and ρ, on dorsal shield of tenth abdominal segment. Seta α absent. Each seta, γ, δ, and ρ, less than half width of base of subconical process. Seta γ slightly longer than ρ. Three setae, ω, ω', and ω'', on single pinaculum ventral to σ.

Panorpa nuptialis Gerstaecker, 1863

Ten fourth instar larvae examined (reared from adults collected in Mississippi County, Missouri, G. W. Byers rearing lot no. 150). Fourth instar larva 18-20 mm long. On lateral surface of head S_1 the longest (Fig. 24). Seta SIV approximately equal to SV, and SVII twice as long as SVIII.

Seta γ on prothoracic shield broader at base than at pointed tip (Fig. 25). On posterior margin of shield ρ' not in a straight line with β and ρ. Seta ρ 1.5-2 times length of β and 2-3 times length of ρ'. Seta η located on anterior margin of shield and in a straight line with γ, ϵ, and α. Length of rectangular pinaculum with π and υ three times its width. Seta υ about three-fourths length of π, and υ' and π' equal.

On dorsal shield of metathorax ρ two times length of β which is slightly longer than ρ' and δ. In some specimens ρ' longer than δ and in others ρ' and δ equal. Seta ρ' closer to ρ than to α. An extra seta near pinaculum with ϵ and ϵ' and almost in a straight line with

these two setae. Seta κ three times length of η, and γ four times length of γ'. Relative lengths of setae π and υ same as on prothorax. Pinaculum with π and π' extends ventrally into a bluntly pointed lobe which is only faintly visible in some specimens.

On each of first seven abdominal segments seta ρ longer than β which is slightly longer than ρ' and δ which are equal. Seta σ almost twice as long as τ and ω which are equal.

Three setae, γ, δ, and α, on dorsal shield of eighth abdominal segment. Seta ρ absent. Seta γ and δ each less than width of base of subconical process. Seta π' half to three-fourths length of π.

Four setae, γ, δ, α, and ρ, on dorsal shield of ninth abdominal segment (Fig. 26). Setae γ, δ, and ρ about the same length and each less than width of base of subconical process. Seta α minute. An extra seta on posterior edge of shield between ρ and γ, and less than half their length. Seta π minute. Two setae, ω and ω', on single ventral pinaculum; seta ω 1.5 times length of ω'.

On dorsal shield of tenth abdominal segment are four setae, γ, δ, α, and ρ (Fig. 27), each shorter than width of base of subconical process. In some specimens γ slightly longer than ρ. Setae ω, ω', and ω'' located on a single ventral pinaculum.

Panorpa subulifera Byers, 1962

Eleven fourth instar larvae (reared from adults collected at Mountain Lake Biological Station, elevation 3950 feet, Giles County, Virginia, G. W. Byers rearing lot no. 153). Fourth instar larva 11-14 mm long. On lateral surface of head S_1 longest seta and almost twice as long as S_4, shortest seta (Fig. 28). On dorsal surface of head SVII twice as long as SVIII. In set SI outside pair three times as long as inside pair.

Seta γ on prothoracic shield equal in width throughout (Fig. 29). On anterior margin of shield seta η in a straight line with γ, ϵ, and α. Midway between η and spiracle is an extra puncture, but no seta. On posterior margin of shield ρ' not in a straight line with β and ρ. Seta ρ slightly longer than β and 2-3 times as long as ρ'. Length of rectangular pinaculum with π and υ 2-2.5 times its width. Seta υ three-fourths length of π and three times or more length of υ'. Also, π three times or more length of π'.

Seta ρ on dorsal shield of metathorax (Fig. 30) three times as long as β which is 1.5-2 times length of ρ' which is longer than δ. Seta ρ' usually closer to ρ than to α. In some specimens an extra seta located near pinaculum with ϵ and ϵ' almost in a straight line with them. Seta κ four times length of η. Relative lengths of π, π', υ, and υ' same as on prothorax. Pinaculum with π and π' extends ventrally into faintly visible bluntly pointed lobe.

On each of first seven abdominal segments seta ρ longest, β two times length of ρ' and δ which are equal. Seta σ about 1.5 times length of τ and ω which are equal.

Two setae, γ and δ, on dorsal shield of eighth abdominal segment (Fig. 31). Seta ρ absent. Rarely α may be present. Each seta, γ and δ, shorter than width of base of subconical process, rarely half or less than its width. Seta π two times length of π'.

On dorsal shield of ninth abdominal segment three setae, γ, δ, and ρ, approximately equal and each less than half width of base of subconical process. Seta α absent. Seta π either absent or minute. Setae ω and ω' on single pinaculum ventral to σ. Seta ω' minute.

On dorsal shield of tenth abdominal segment three setae, γ, δ, and ρ, equal in length and each about half width of base of subconical process. Seta α absent.

Three setae, ω, ω', and ω'', on pinaculum ventral to σ.

INTRASPECIFIC VARIATION

The number of setae on *Panorpa* larvae varies within species. An extra seta may appear on any segment on either side. Often there are one to three extra setae on the anterior or posterior margin of the dorsal shield of the prothorax or extra setae on the dorsal shields of the mesothorax, metathorax, or eighth abdominal segment. Less often, extra setae occur on the first seven abdominal segments, but rarely on their smaller lateral pinacula. Setae are often missing from any of several pinacula or the dorsal shield on either side of the larva. In many larvae, a seta may be missing on one side but present on the other, or there may be an extra seta on one side and not on the other. Because of this variation, it is advisable to check both sides of a larva when using the key. A seta is rarely absent on both sides of the larva, and an extra seta is only rarely present in the same place on both sides. In cases of doubtful identification, it is advisable to check the species description.

The size range of larvae in any one instar varies from species to species. However, size has not been used to separate species because the larvae examined were laboratory-reared and are, in some instances, known to be smaller than larvae of corresponding stages under natural conditions.

There is much variation in the coloration of the specimens, but this is perhaps due to the methods of preservation and not to natural variation. There is also a large amount of variation in the number of facets per eye, even between the left and right eyes of the same specimen. Difficulty in distinguishing clearly and counting all the facets could account for some of the variation recorded here.

TENTATIVE KEY TO FOURTH INSTAR *PANORPA* LARVAE

1. Setae δ and γ on eighth, and δ, γ, and ρ on ninth and tenth abdominal segments each longer than width of base of respective subconical process; ρ' in a straight line with β and ρ on pronotum (Figs. 13-14) ..... *lugubris*

   Setae δ and γ on eighth, and δ, γ, and ρ on ninth and tenth abdominal segments each shorter than width of base of respective subconical process; ρ' usually not in a straight line with β and ρ on pronotum 2

2. Following combination of characteristics present: setae γ, δ, and ρ on ninth and tenth abdominal segments each distinctly longer than half but shorter than entire width of base of subconical process; seta η on anterior margin of pronotum; one or more supernumerary setae or setal punctures on dorsal shield of ninth abdominal segment between γ and ρ (Figs. 25-27) ..... *nuptialis*

   Previous combination of characteristics lacking 3

3. Pinaculum with π and π' on metathorax without lobe-like extension; no extra setae or setal punctures near γ and ρ on ninth abdominal segment (Fig. 4) 4

   Pinaculum with π and π' on metathorax with lobe-like extension (Fig. 1) 7

4. Setae ω and ω' on ninth abdominal segment almost equal in length and on two separate pinacula *or* seta ω' absent; seta ρ' equidistant from ρ and α on metathorax (Figs. 4, 6) 5

   Seta ω' minute and much shorter than ω on ninth abdominal segment, both on a single pinaculum; ρ' closer to ρ than to α on metathorax (Fig. 18) ..... *helena*

5. Extra minute seta near pinaculum with ϵ and ϵ' on metathorax; ω' present and almost equal in length to ω on ninth abdominal segment (Figs. 4, 6) ..... *anomala*

   Extra seta near pinaculum with ϵ and ϵ' on metathorax usually absent; ω' on ninth abdominal segment absent 6

6. Seta ρ 2 times length of β on metathorax; ω'' on tenth abdominal segment present ..... *banksi*

   Seta ρ 2.5-3 times length of β on metathorax; ω'' on tenth abdominal segment absent ..... *mirabilis*

7. Seta η on anterior margin of pronotum; on metathorax ρ' closer to ρ than to a, and β one-third length of ρ; no extra seta or setal puncture near γ and ρ on dorsal shield of ninth abdominal segment (Figs. 29-31) ..... *subulifera*

   Previous combination of characteristics lacking 8

8. Setae δ and γ on eighth abdominal segment each longer than one-half but shorter than entire width of base of subconical process (Fig. 21) 9

   Setae δ and γ on eighth abdominal segment each shorter than one-half width of base of subconical process (Fig. 16) 10

9. No extra seta near pinaculum with ϵ and ϵ' on metathorax; a absent on second abdominal segment .. *claripennis*

   Extra seta near pinaculum with ϵ and ϵ' on metathorax; a present on second abdominal segment (Fig. 15) ..... *latipennis*

10. Setae ω and ω' almost equal on ninth abdominal segment; extra seta (if present) near pinaculum with ϵ and ϵ' on metathorax not in a straight line with them; a absent from both second and eighth abdominal segments (Figs. 7-10) ..... *carolinensis*

    Seta ω' minute and much shorter than ω on ninth abdominal segment; extra seta (if present) near pinaculum with ϵ and ϵ' on metathorax in a straight line with them; a present on either second or eighth abdominal segment or on both 11

11. Extra seta near γ and ρ on posterior margin of dorsal shield of ninth abdominal segment; on metathorax β one-third length of ρ (Figs. 11-12) ..... *flexa* (?)

    No extra seta near γ and ρ on posterior margin of dorsal shield of ninth abdominal segment; on metathorax β half length of ρ 12

12. No extra seta near pinaculum with ϵ and ϵ' on metathorax; a present on eighth abdominal segment; on second abdominal segment β longer than ρ'; on metathorax ρ' equidistant from ρ and a (Figs. 19-21) ..... *nebulosa*

    Extra minute seta present near pinaculum with ϵ and ϵ' on metathorax; a absent from eighth abdominal segment; on second abdominal segment ρ' equal to β; on metathorax ρ' closer to ρ than to a (Figs. 1-3) ..... *acuta*

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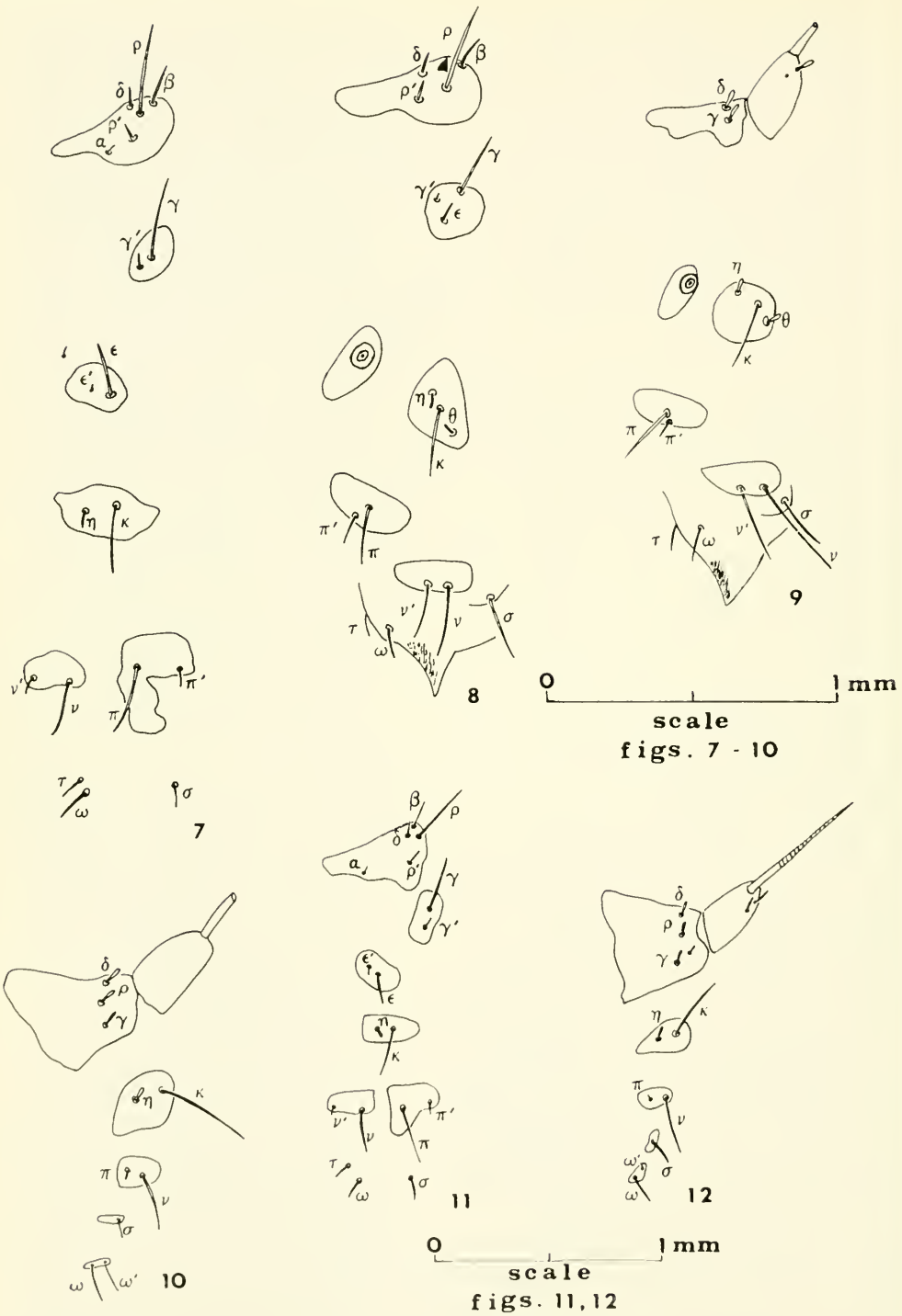
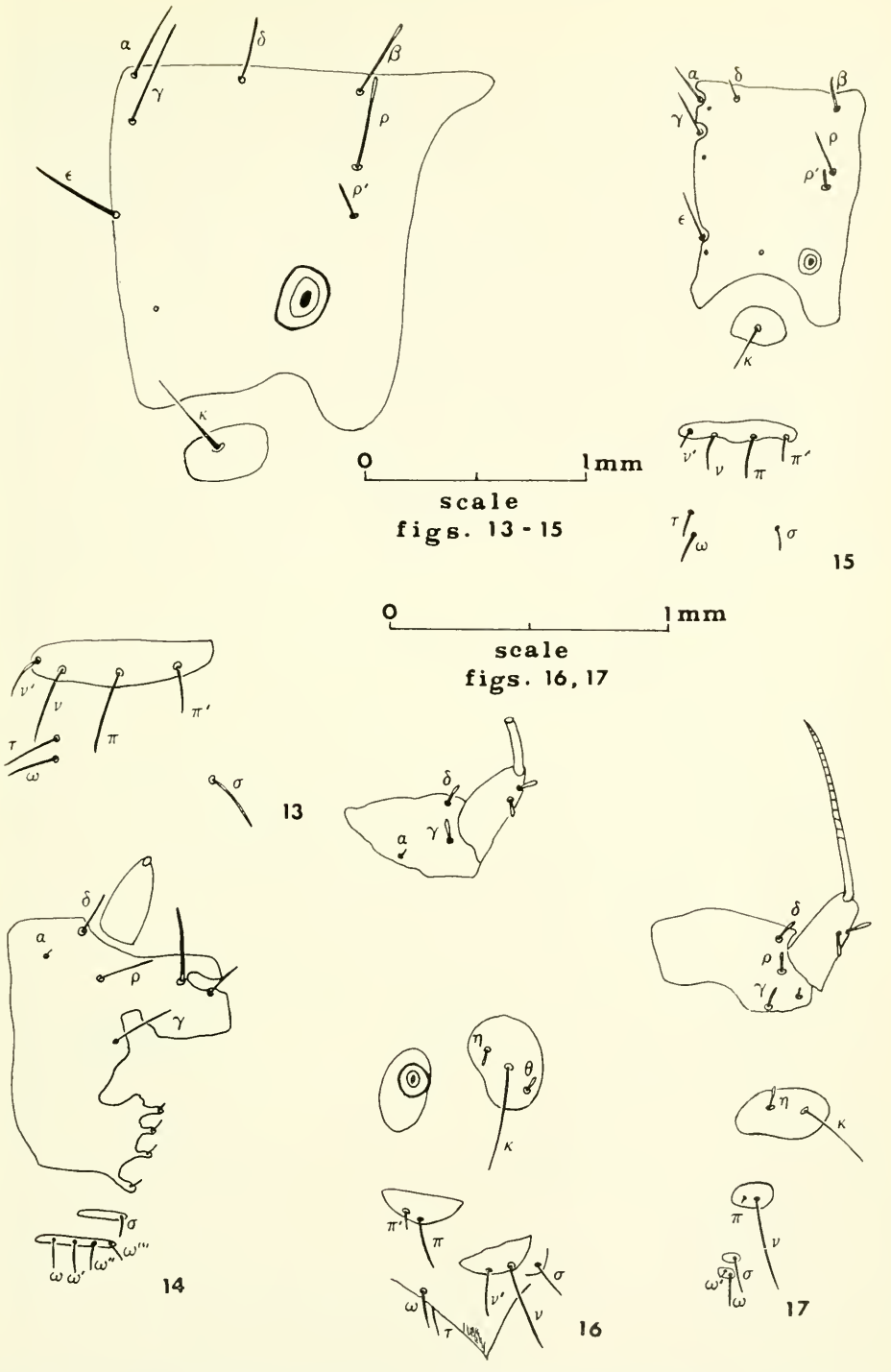
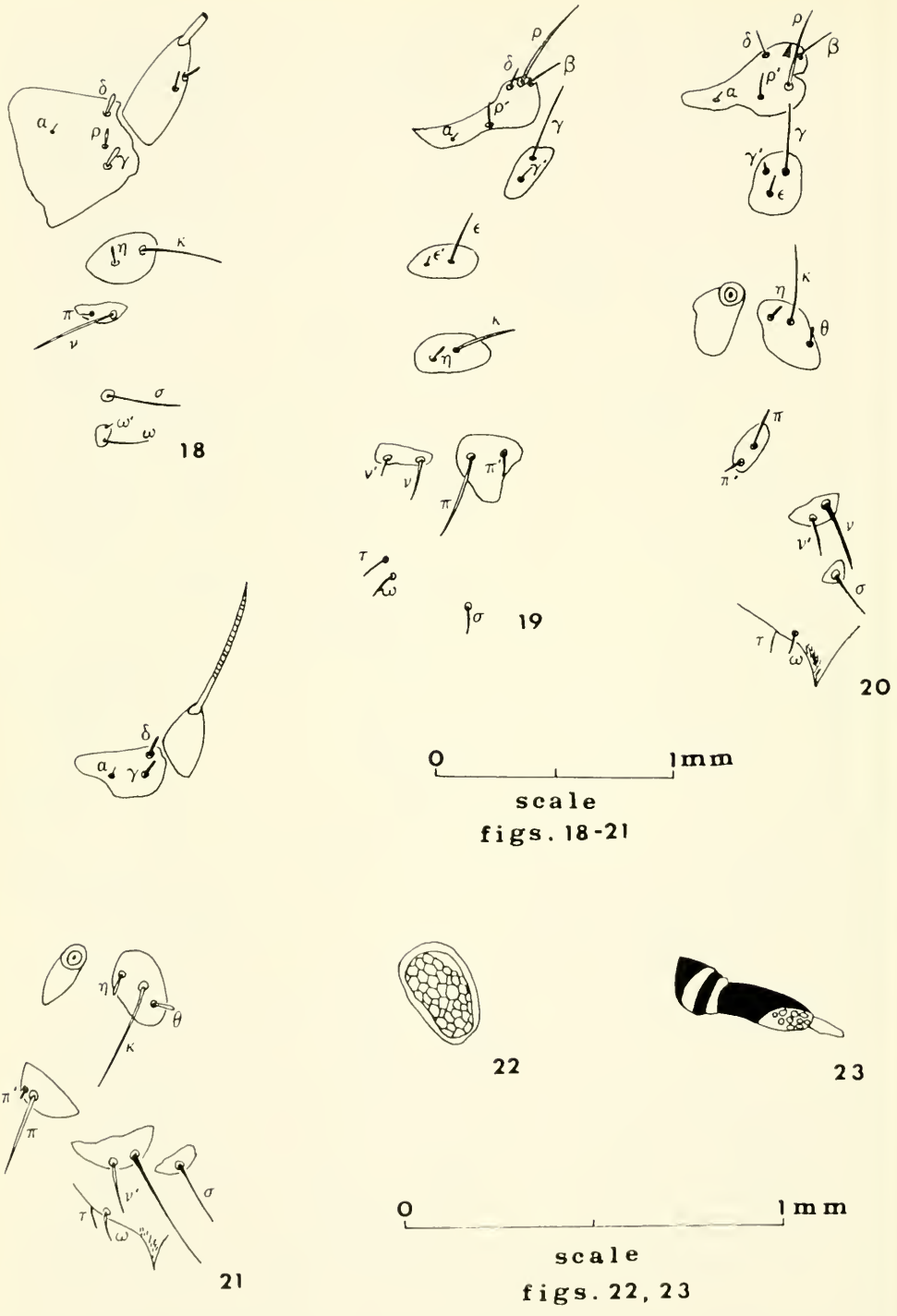
FIGS. 1-6. **1,** *P. acuta,* metathorax; **2,** *P. acuta,* second abdominal segment; **3,** *P. acuta,* eighth abdominal segment; **4,** *P. anomala,* metathorax; **5,** *P. anomala,* eighth abdominal segment; **6,** *P. anomala,* ninth abdominal segment. (Orientation: lateral view; anterior end is to the left.)



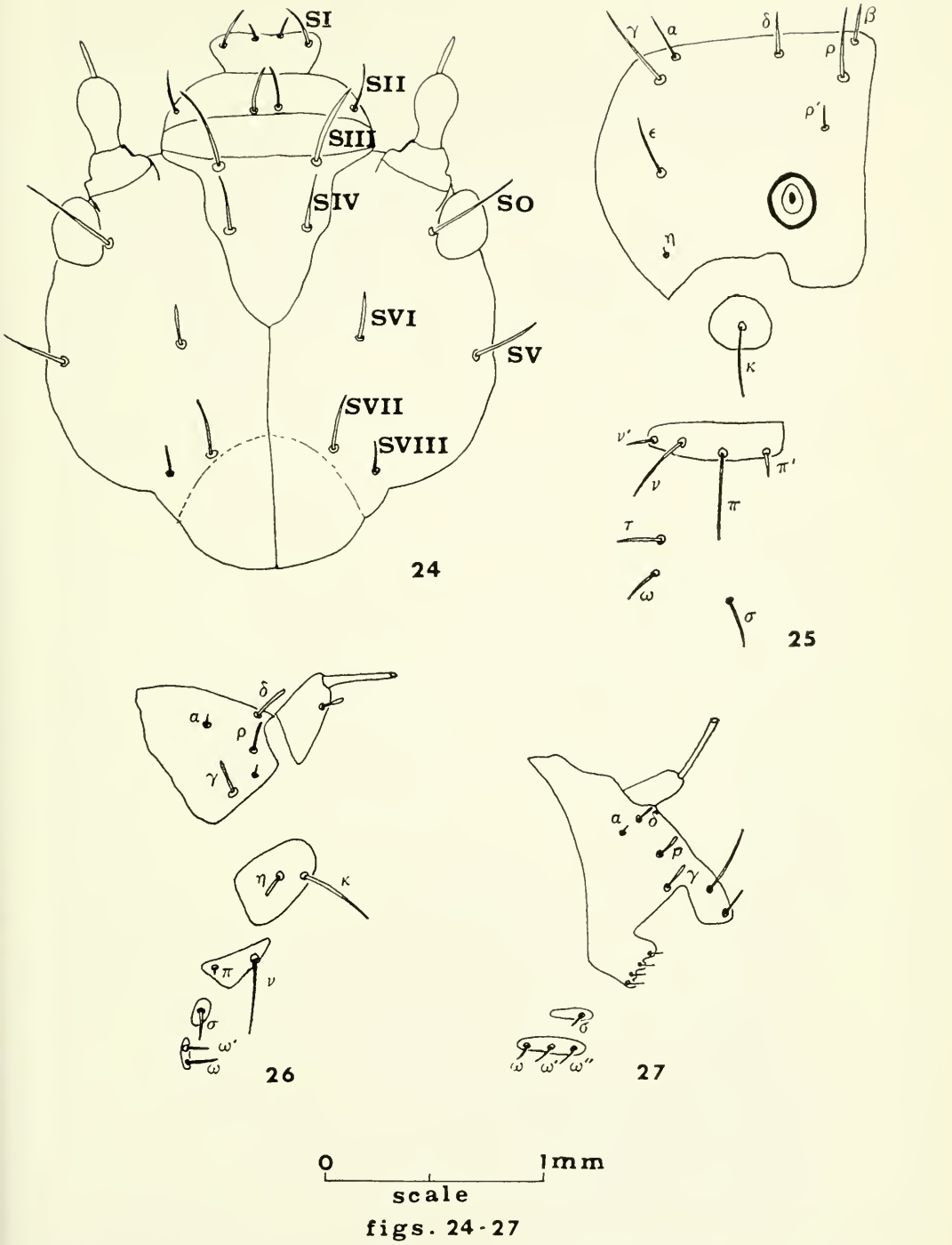
FIGS. 7-12. **7**, *P. carolinensis*, metathorax; **8**, *P. carolinensis*, third abdominal segment; **9**, *P. carolinensis*, eighth abdominal segment; **10**, *P. carolinensis*, ninth abdominal segment; **11**, *P. flexa* (?), metathorax; **12**, *P. flexa* (?), ninth abdominal segment. (Orientation is as for Figs. 1-6.)



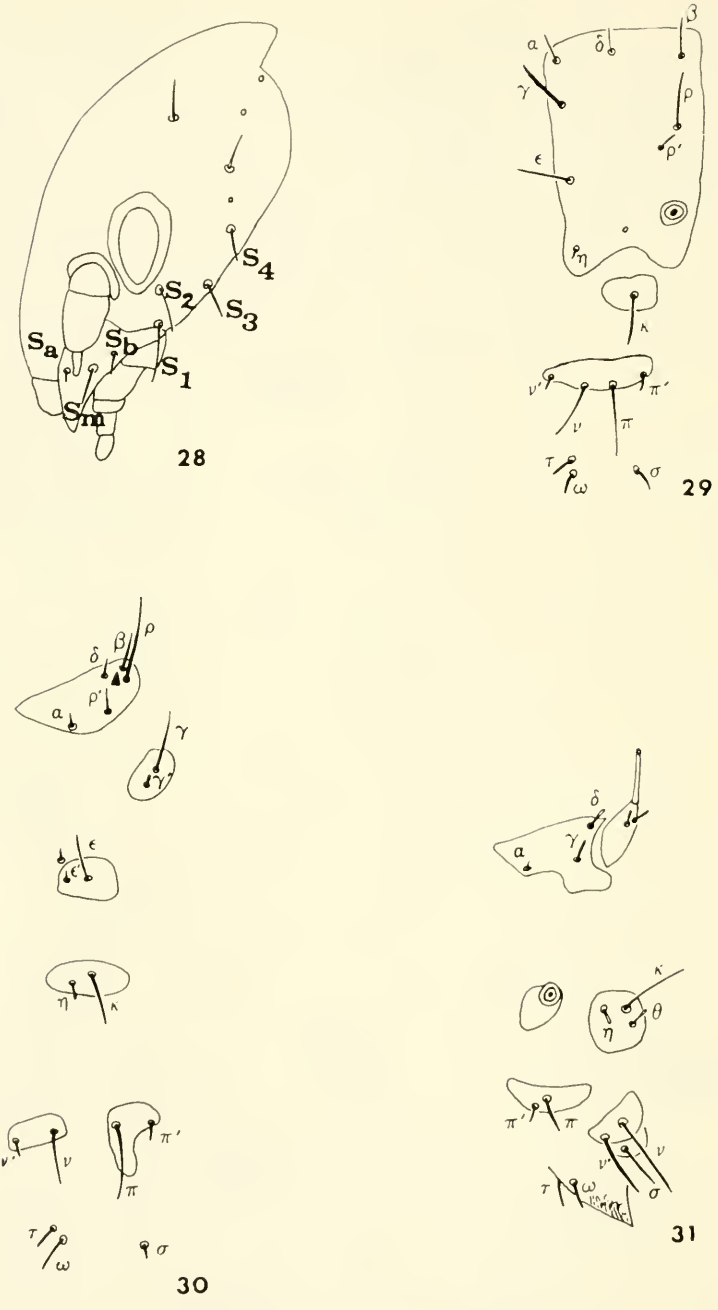
FIGS. 13-17. **13,** *P. lugubris,* prothorax; **14,** *P. lugubris,* tenth abdominal segment; **15,** *P. latipennis,* prothorax; **16,** *P. latipennis,* eighth abdominal segment: **17,** *P. latipennis,* ninth abdominal segment. (Orientation is as for Figs. 1-6.)



FIGS. 18-23. 18, *P. helena*, ninth abdominal segment; 19, *P. nebulosa*, metathorax; 20, *P. nebulosa*, first abdominal segment; 21, *P. nebulosa*, eighth abdominal segment; 22, *P. nebulosa*, eye; 23, *P. nebulosa*, antenna. (Orientation is as for Figs. 1-6.)



FIGS. 24-27. **24,** *P. nuptialis,* dorsal view of head; **25,** *P. nuptialis,* prothorax; **26,** *P. nuptialis,* ninth abdominal segment; **27,** *P. nuptialis,* tenth abdominal segment. (Orientation of Figs. 25-27 is as for Figs. 1-6.)



FIGS. 28-31. **28**, *P. subulifera,* head; **29**, *P. subulifera,* prothorax; **30**, *P. subulifera,* metathorax; **31**, *P. subulifera,* eighth abdominal segment. (Orientation is as for Figs. 1-6.)

S-NA-L[awrence]

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

A CAECILIAN MISCELLANY

By
EDWARD H. TAYLOR

Vol. 50, No. 5, pp. 187-231 November 30, 1973

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A Caecilian Miscellany

Edward H. Taylor

A Caecilian Miscellany

Edward H. Taylor*

INTRODUCTION

Since the publication in 1968 of my general work "Caecilians of the World," I have had the fortune to examine and take data from more than 200 specimens that were not available to me previously. I have also found occasion to re-examine a number of forms previously recorded. As many species are poorly known from a few specimens and in many cases from only single type-specimens, it is pertinent that all new information be placed on record. This paper reports on these observations and may be regarded as supplemental to my monograph. It contains in addition a few corrections of errors in that work.

It is to be hoped that herpetological collectors in the field will make greater effort to discover more of these elusive creatures even at the expense of a spade and the necessary efforts.

I am under considerable obligation to the several curators of museum collections who have been kind enough to lend me specimens here reported.

The following species are discussed or described in this paper:

Ichthyophis humphreyi sp. nov.
Ichthyophis kohtaoensis Taylor
Ichthyophis mindanaoensis Taylor
Typhlonectes natans (Fischer)
Typhlonectes obesus Taylor
Nectocaecilia ladigesi Taylor
Chthonerpton indistinctum (Reinhardt and Lütken)
Caecilia abitaguae Dunn
Caecilia attenuata Taylor
Caecilia bokermanni Taylor
Caecilia corpulenta Taylor
Caecilia disossea Taylor
Caecilia dunni Hershkovitz
Caecilia inca sp. nov.
Caecilia leucocephala Taylor
Caecilia mertensi sp. nov.
Caecilia nigricans Boulenger
Caecilia perdita Taylor
Caecilia tentaculata Linnaeus
Caecilia tenuissima sp. nov.
Oscaecilia bassleri (Dunn)
Oscaecilia equatorialis sp. nov.
Oscaecilia ochrocephala ochrocephala (Cope)
Microcaecilia albiceps (Boulenger)
Luetkenotyphlus brasiliensis (Lütken)
Herpele squalostoma (Stutchbury)
Schistometopum thomense (Barboza du Bocage)
Siphonops annulatus (Mikan)
Siphonops hardyi Boulenger
Siphonops paulensis Boettger
Dermophis gracilior (Günther)
Dermophis mexicanus eburatus Taylor
Geotrypetes grandisonae Taylor
Geotrypetes seraphini congoensis Taylor
Uraeotyphlus menoni Annandale
Scolecomorphus vittatus Boulenger

The following museum abbreviations are used:

AMNH: American Museum of Natural History, New York.

BMNH: British Museum of Natural History, London.

CAS: California Academy of Sciences, San Francisco.

DSBM: Division of Systematic Biology, Museum, Stanford, California.

EHT-HMS: Edward H. Taylor-Hobert M. Smith Herpetological Collection, Lawrence, Kansas.

* Research Associate, University of Kansas Museum of Natural History.

FMNH: Field Museum of Natural History, Chicago.

KUMNH: University of Kansas Museum of Natural History, Lawrence, Kansas.

LACMNH: Los Angeles County Museum, California.

UMMZ: University of Michigan Museum of Zoology, Ann Arbor.

USNM: United States National Museum, Washington, D.C.

ZSIC: Zoological Survey of India, Indian Museum, Calcutta, India.

ZSZM: Zoologische Statsinstitut und Zoologische Museum, Hamburg, Germany.

Ichthyophis humphreyi sp. nov.
(Figs. 1-3)

HOLOTYPE: EHT-HMS No. 8378. Type-locality and collector unknown, but presumed to be from southern Asia or a neighboring island of Indonesia. It is a larval specimen, probably in its second year.

DIAGNOSIS: Body and tail folds (primaries and secondaries) total 415-422 (depending on the level on the circumference where the count is made). Those on the anterior three fourths of the body form two angles (dorsal and ventral) in passing around the body; in the posterior fourth they tend to lose the angles and pass di-

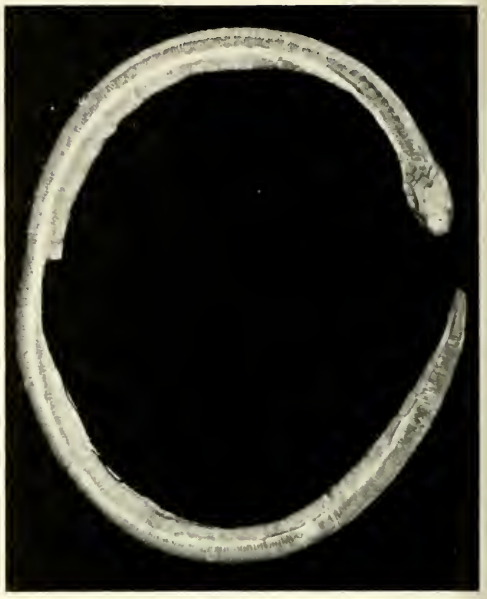

FIG. 1. *Ichthyophis humphreyi* sp. nov. Type. EHT-HMS No. 8378. Type-locality, not known. Lateral view (dorsal of head). Body injured near middle. Length, 205 mm.

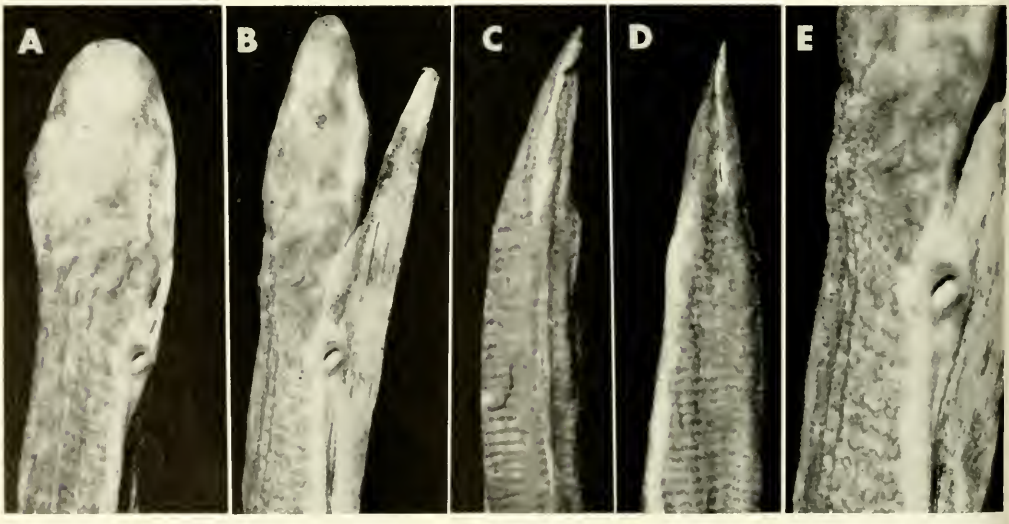

FIG. 2. *Ichthyophis humphreyi* sp. nov. Type. EHT-HMS No. 8378. Type-locality, unknown. **A**, Dorsal view of head; **B**, lateral view of head; **C**, dorsal view of caudal region; **D**, ventral view of caudal region; **E**, neck area showing gill and dermal glands in folds.

rectly around the body. A light stripe from before eyes to vent laterally.

Description of the Holotype: The larva has a length of 205 mm, a head width of 6 mm, a body width of about 4.2 mm. The height in much of the body is 7 mm. The head seemingly is flattened. The eye is in a distinct socket. The tentacle has not yet formed a tentacular aperture but the aperture is represented only by a slight depression closely preceding the eye. The nostrils are not visible from directly above the head, but are indicated by slight elevations on the periphery of the snout (a juvenile character). The snout extends perhaps less than half a millimeter beyond the mouth. I find no trace of the lateral line system remaining. The choanae are elongate, lateral, directed outward and widely separated. The tongue is as yet poorly developed. No narial plugs are present. The vent is longitudinal. Primary and secondary folds together are 415-422. There are 112 vertebrae. About 12 are confined to the tail, the terminal folds being poorly defined. Tail strongly compressed, with a fin several millimeters long dorsally, and passing around the tip. Dermal glandules are dimly evident on many of the folds. They appear more or less circular and slightly raised. The distinctness of these externally is probably due to fixation. These are scarcely discernible even under a lens.

Scales seemingly have not yet developed; no species of the Ichthyophiidae is known lacking scales in the adults.

The dental formulae are: premaxillary-maxillary, 17-1-17; prevomeropalatine, 20-1-20; dentary, 19-19; splenial, 9-10. There is no evidence of group-loss or group-replacement of teeth. It is probable that the adults will have a few more teeth in each series.

Measurements in mm: Length, total, 205; tail, 5.5; width of head, 6; width of body, about 4.2; height of body, 7; body width in length, about 49 times; tail length in total length, about 37 times.

Color: At present the body is deep brown. A whitish or yellowish lateral stripe from in front of the eye to vent. There are no distinguishable white spots on the head. Anterior part of head vaguely lighter. There is a whitish spot at vent.

Remarks: At the present time there are two tiny skin folds that originate in the nuchal region and pass, occasionally broken, posteriorly along the dorsal part of the body. At places these are not present but reappear and may be seen near the

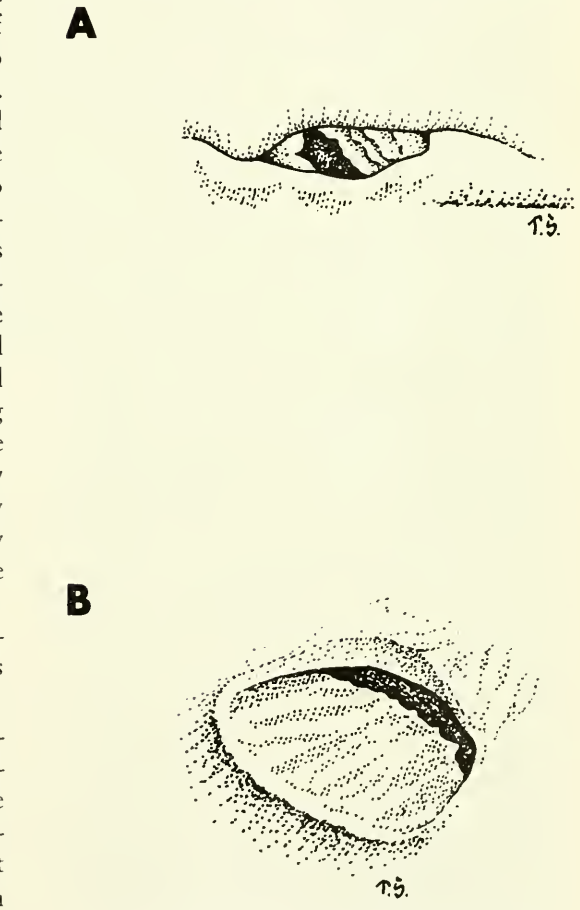

Fig. 3. A, Appearance of one gill slit of a single pair in larvae of species of the Ichthyophiidae other than *Ichthyophis humphreyi*. B, Appearance of a gill slit from the single pair in *I. humphreyi*, in larvae of similar age as preceding (from type). Anterior is to the right.

posterior part of the body. These folds may be the result of the fixation.

The character of the large single gill slit on each side differs from that of all other caecilian larvae that I have examined. Figure 3 demonstrates the difference between the two types of larval gills.

The number of folds (primary and secondary together) exceeds that of any other known species.

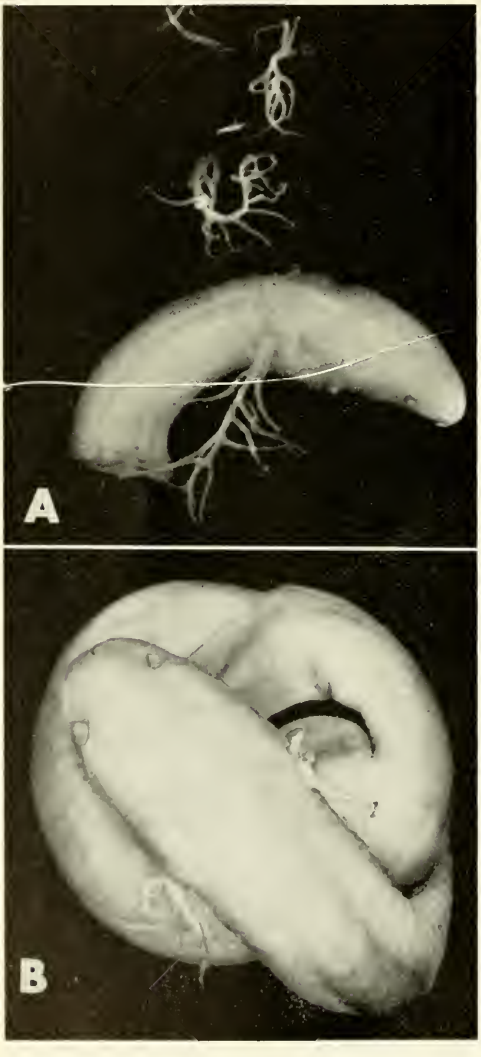

FIG. 4. *Ichthyophis kohtaoensis* Taylor. A, Embryo removed from egg showing three pairs of gills, two broken from right side, all three from left side. B, Embryo in position in egg, the gills evident laterally. Both are enlarged.

The species is named in honor of Dr. Philip Humphrey, Director of the Museum of Natural History, Kansas University, in recognition of the courtesies extended to me at the Museum.

Ichthyophis kohtaoensis Taylor

(Fig. 4)

The gills of the species of this genus in the specimens that have been available are developed and reabsorbed in the egg before the young hatch. Figure 4B here presented shows an embryo as seen through the transparent egg cover, the gills being more or less obvious. In Figure 4A the embryo has been removed from the egg. There are three lateral pharyngeal gills of varying size. On the left side the gills are broken away from the pharyngeal region, on the right side the largest one is still attached. The species retains a single gill slit until it emerges from its water environment and transforms. (Certain of the other species of this genus retain two gill slits until they transform.) As yet I have not seen embryonic gills of the young of the Scolecomorphidae or of either of the subfamilies of the Caeciliidae.

Ichthyophis mindanaoensis Taylor

(Figs. 5-6)

Ichthyophis mindanaoensis Taylor, Univ. Kansas Sci. Bull., vol. 40, No. 4, 1960, pp. 69-74, figs. 13-15. Type-locality, Todaya, Mt. Apo, Mindanao.

I have examined several more specimens of this species from Mindanao, all from an area distant from the type-locality. A reexamination of specimen DSBM No. 20931 (now in the California Academy of Sciences) shows an error in the count of the combined primary and secondary folds. The correct numbers are, dorsal count 326, ventral count 316. Thus the total variation of the series of folds is from about 287 to 326, a difference of about 39 which is equivalent to about 13 primary folds.

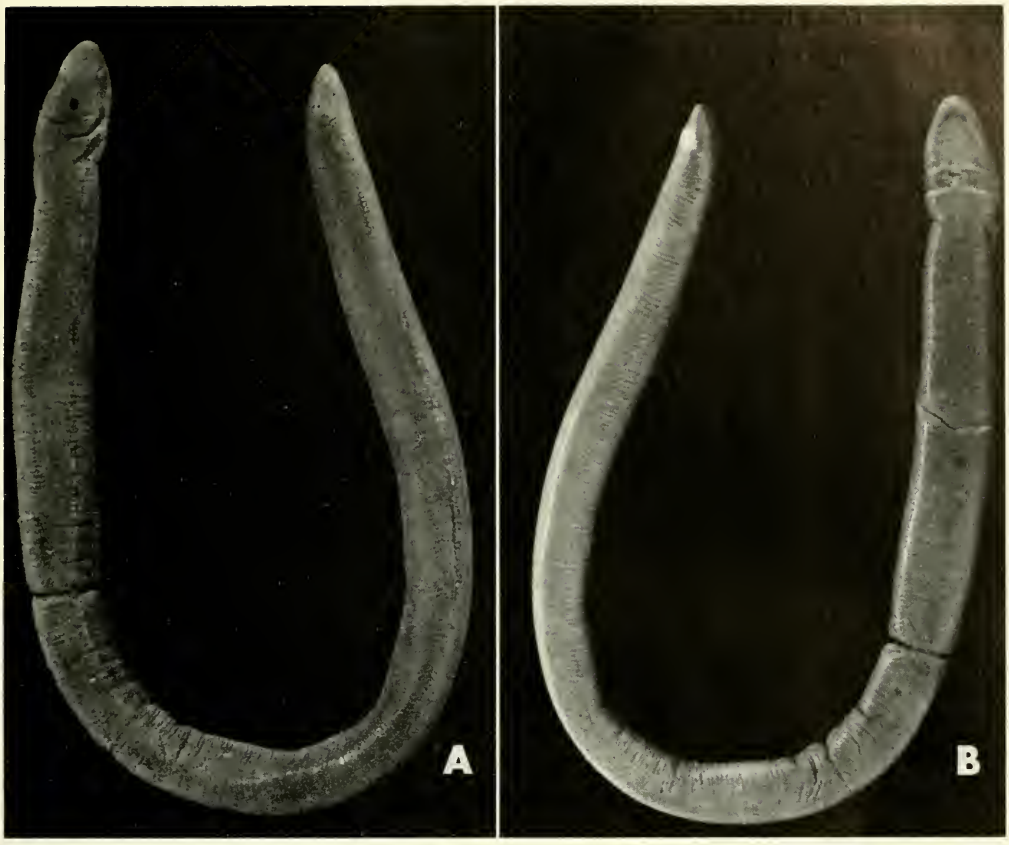

Fig. 5. *Ichthyophis mindanaoensis* Taylor. CAS No. 20922. Misamis Occidentalis Province, Mindanao, P.I. Bank of Dapitan River, 11-12 km SE Buena Suerte, New Pinan, west side Dapitan Peak, ca 4,000 ft. **A,** Dorsal view; **B,** ventral view. Length, 275 mm.

The type is from Mt. Apo at an elevation of about 2,800 ft. The other specimens here studied are from Dapitan Peak in the province of Zamboanga, Mindanao, at an elevation between 2,000 and 4,000 ft.

Transformation of larvae seemingly occurs the second or third year of life. This species differs from *I. glandulosus* Taylor in having 111-116 vertebrae compared with 102-104; the combined folds greater in number, 287-326 compared with 273-297; and splenial teeth in adults 3-3, compared with 11-11. *I. glandulosus* presumably transforms during the first year of life instead of the second or later. *I. glandulosus* is known as a lowland form.

Typhlonectes natans (Fischer)

(Fig. 7)

Caecilia natans Fischer, Arch. für Naturg., Jahr. 46, vol. 1, 1880, pp. 217-218, pl. 8, figs. 5-7. Type-locality, Río Cauca, Colombia.

In species of caecilians it is not often that a large series of specimens is available from a single locality. Thus information is rarely available on the amount or degree of variation obtaining in a species in a given locality. Data taken from such material do not include variation resulting from different geographical conditions such as elevation, and climate or other environmental factors.

It has been my good fortune to have

TABLE 1. Data on *Ichthyophis mindanaoensis* (measurements in mm).

Locality	Mt. Apo, Mind. Type	Mt. McKinley, Mind. Paratype	Mt. Dapitan, Mind.	Mt. Dapitan, Mind.	Mt. Dapitan, Mind.	Mt. Dapitan, Mind.	Mt. Dapitan, Mind.
Number*	50958	50957	20930	20921	20934	20928	20929
Total length	276	283	—	274	260	245	311
Body width	9.8	—	9.	10.	10.2	9.3	12.
Head width	9.3	—	9.	9.8	9.8	—	9.9
Snout tip to 1st groove	12.	—	10.	11.6	12.2	—	13.
Snout tip to 2nd groove	15.	—	12.	13.9	14.2	—	16.
Snout tip to 3rd groove	20.	—	16.1	17.2	17.3	—	19.7
Eye to tentacle	1.5	—	1.3	1.65	1.5	—	1.75
Tentacle to nostril	3.6	—	3.3	3.3	3.8	—	3.8
Folds, dorsal count	308	308	305	310	317	316	—
Premax-max teeth	25-26	25-26	24-25	26-26	26-25	27-25	—
Prevom-palatine teeth	24-24	24-24	20-21	23-23	23-24	23-22	—
Dentary teeth	17-18	17-18	19-20	19-19	23-22	22-22	—
Splenial teeth	8-8	8-8	8-9	9-10	10-10	10-10	—
Post. scale rows	3	3	3	3	3	3	3
Vertebrae	111	113	—	—	—	—	—
Elevation, ft.	2,800	2,000	3,700	—	—	2,500	—

* Type and paratype, FMNH; others, CAS.

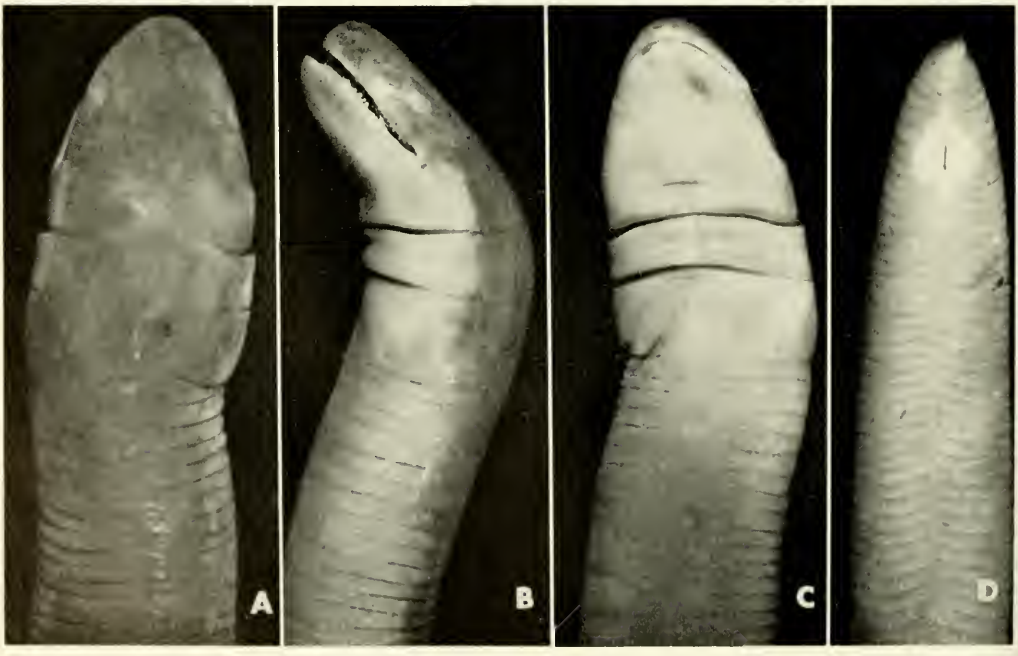

FIG. 6. *Ichthyophis mindanaoensis* Taylor. CAS No. 20922. Misamis Occidentalis Province, P.I. **A,** Head and neck, dorsal view; **B,** head and neck, lateral view; **C,** head and neck, ventral view; **D,** subcaudal region.

Fig. 7. *Typhlonectes natans* (Fischer). Barranquilla, Colombia. Dorsal (right) and ventral views.

been given the privilege by Dr. John Wright of studying a large series of specimens (120) acquired by the Los Angeles County Museum of Natural History from near Barranquilla at the mouth of the Magdalena River, Colombia.

In my previous work (Taylor, 1968) I prepared a table of variation in 25 specimens that were available to me at that time from various points in its range. These varied in length from 140 mm to 577 mm, the primary folds from 83 to 95 with a mean of 90.

In the present lot of specimens the primary folds vary from 83 to 90 (mean 86), the total length from 139 to 380 mm. The earlier series had 15 of the 25 specimens larger than the largest of this series.

Variation in the dental series is not great. Such as obtains has been proved in many species to be a matter of age; that is, more teeth are added as the animal increases in age and size.

Typhlonectes obesus Taylor

(Figs. 8-9)

Typhlonectes obesus Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 253-255, fig. 129. Type-locality, "Maues, Brasil."

The present species was described from a single pregnant female whose body was somewhat distorted by the embryos and it did not disclose the normal degree of body compression. I have recently been able to study three specimens of this form through the courtesy of the California Academy of Sciences. These are from a Brasilian area not far distant from the type-locality. Data taken from these specimens are compared with the data taken from the type, and the three specimens are figured.

The recently born young still shows the "scar" on the occiput where the embryonic gills attached. There are now no gill slits. The dental series are as yet poorly developed. The head is proportionally wider than in the adult (see Fig. 8C). The dor-

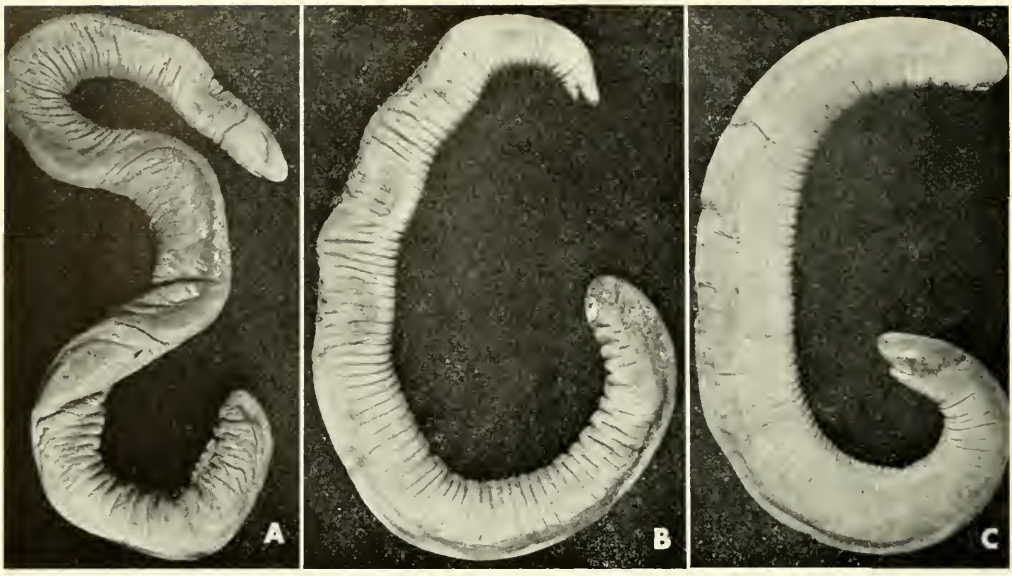

FIG. 8. *Typhlonectes obesus* Taylor. **A,** CAS No. 125422, from "Petite Igarapi, affluent of Rio Jacitara, Lago Grande de Manacapuru, Estado Amazonas, Brasil." Length, 438 mm. **B,** CAS No. 125421, from "Petite Igarape, affluent of Rio Jacitara, Lago Grande de Manacapuru." Length, 290 mm. (Formerly Brussels Mus. No. 2725.) **C,** CAS No. 125423, from "Igarape Pixuna du Lago Januari (rive droit Rio Negro, Maues, Estado Amazonas)." Length, 129 mm; recently born young. (Formerly Brussels Museum No. 2699.)

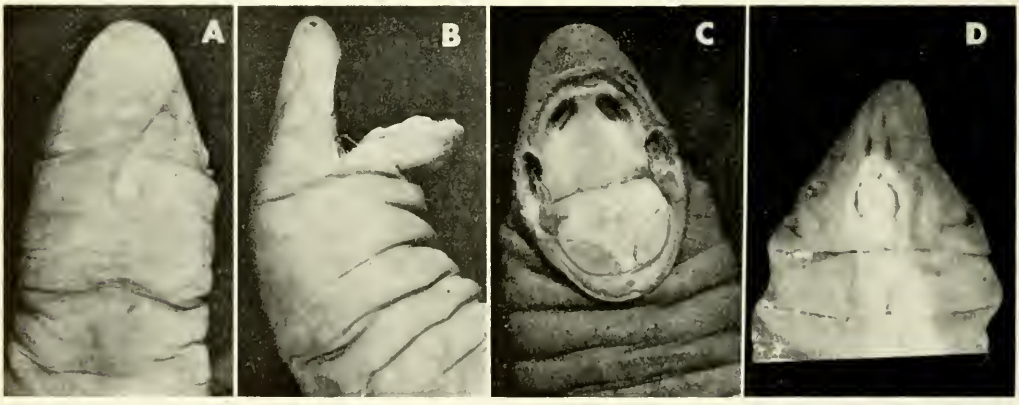

FIG. 9. *Typhlonectes obesus* Taylor. CAS No. 125421. **A-B,** Head; **C,** buccal region; **D,** subterminal area.

sal fin is proportionately higher than in the adult.

It will be observed that body height exceeds body width in both young and adults.

These specimens do not show the same amount of wrinkling as obtained in the type which had been strongly coiled.

Nectocaecilia ladigesi Taylor

(Figs. 10-11)

Nectocaecilia ladigesi Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 275-278, figs. 139, 142. Type-locality, "Bocco do Moju" (Rio Moju near mouth, Pará, Brasil); Univ. Kansas Sci. Bull., 1970, vol. 48, no. 24, pp. 859-869, fig. 3.

I have had the good fortune to examine 3 recently collected specimens of *N.*

Table 2. Data on *Typhlonectes obesus* (measurements in mm).

Museum Number*	AMNH 71434	CAS 125421	CAS 125422	CAS 125423
Total length	373	290	438	129
Width of head	12	10.2	15.2	6
Width of body, approx.	32	15	18	7.5
Height of body	32±	19	29±	11.6
Width in length	12	19	24	17
Snout projects	3.	2.9	3.4	2.9
Eye to tentacle	5.2	3.5	3.6	2.7
Nostril to tentacle	0.7	0.7	0.65	0.3
Primary folds	88	86	83	77
Secondary folds	0	0	0	0
Premax-max teeth	20-20	20-1-21	22-1-23	—
Prevom-palatine teeth	18-20	19-1-19	23-1-24	—
Dentary teeth	18-(18)	18-18	19-18	—
Splenial teeth	5-5	5-5	7-7	—
Dorsal fin height	9.	—	—	—
Vertebrae	101	—	—	—
Sex	♀	♀	♀	♂

* Localities. No. 71434: "Junction of the Rio Camiña and Maues Gaucu rivers, Estado Amazonas, Brasil." No. 125421: "Petite Igarape, affluent of Rio Jacitara, Lago Grande de Manacapuru," Estado Amazonas. (Formerly Brussels Museum No. 2725.) No. 125422: Same as preceding. No. 125423: "Igarape Pixuna du Lago Januari (rive droit Rio Negro, Maues, Estado Amazonas)." (Formerly Brussels Museum No. 2699.)

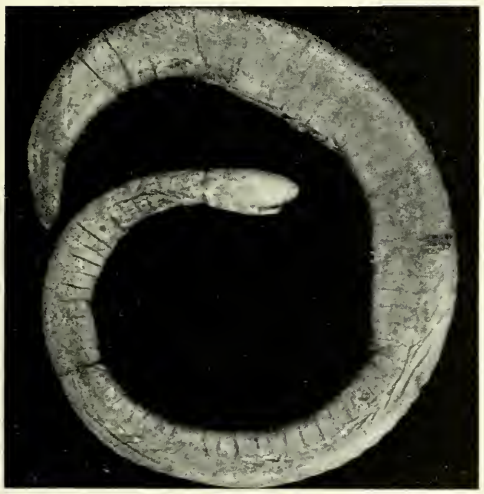

Fig. 10. *Nectocaecilia ladigesi* Taylor. USNM No. 154085. Utinga, Pará, Brasil. Length, 389 mm.

ladigesi—two preserved and one a complete skeleton. The exact locality from which they were obtained is unknown. One other specimen collected by Dr. Philip Humphrey near the type-locality is USNM No. 154085. Data taken from these specimens are compared in Table 3.

The skeleton has a total of 94 vertebrae, which suggests a series of about 87 primary folds, and the total length is about 480 mm. The dental formulae are: premaxillaries 11; maxillaries 16 on the right side (incomplete on the left); prevomers 7; palatines 19 on left (broken on right); dentaries 20; splenials, 8 right, 6+ left. Data on the skull: length, 17 mm; greatest width, 12.2 mm; width between outer edges of eyes, 9.8 mm. Median length of the basisphenoid, 8 mm; greatest length, tip of snout to condyle, 9.1 mm; internal nares surrounded by maxillaries and prevomers. Greatest width of basisphenoid at the level of the wings of basisphenoid, 7.5 mm; snout tip to base of the premaxillary teeth, 2 mm; prefrontals 6 mm long; frontals 4 mm long; parietals 5.6 mm long.

Chthonerpeton indistinctum (Reinhardt and Lütken)

CAS No. 85521 ♂, Edo. Rio Grande do Sul, Brasil, has a head width of 10.4 and

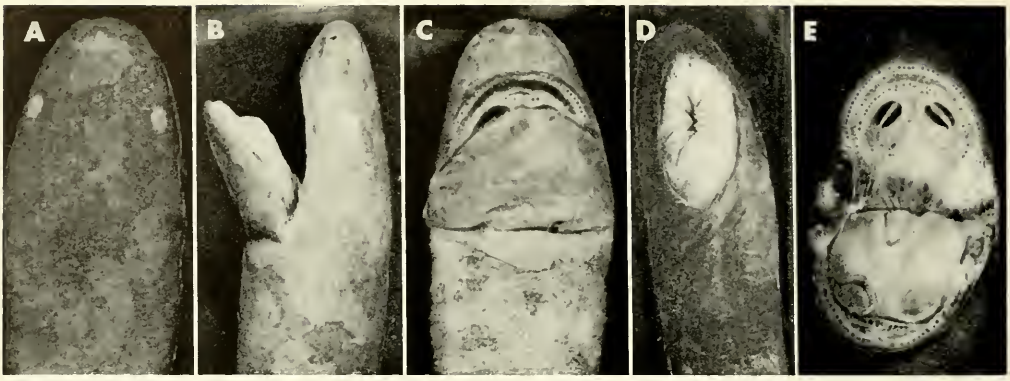

FIG. 11. *Nectocaecilia ladigesi* Taylor. UMMZ No. 129649. Locality, unknown. Length, 419 mm. **A,** Head, dorsal view, width 13.5 mm; **B,** head, lateral view; **C,** head, ventral view; **D,** subterminal region; **E,** buccal area.

a body width of 12.5 mm. Distance of eye to tentacle, 3 mm, to nostril, 1.9 mm. The eye is relatively large with a definite white ring. The nostril is not visible from directly above the head; vent longitudinal with 5 blackish elongate lateral dentacles. Primary folds 77, none complete above or below except posterior 12; no true secondaries. The anal glands conspicuous, whitish in color. Tongue with large plump peripheral plugs. Choanae as large in diameter as the distance between the pair. Tooth formula: premaxillary-maxillary, 17-17; prevomeropalatine, 12-12; dentary, 14-14; splenial, 3-3. Group replacement of teeth (only some of the teeth functioning). Terminal shield moderately large; eye and tentacular aperture connected by a light area. Large whitish spot about the vent area.

Caecilia abitaguae Dunn
(Figs. 12-16)

Caecilia abitaguae Dunn, Bull. Mus. Comp. Zool. Harvard Col., vol. 91, no. 6, 1942, pp. 508-509. Type-locality, Abitagua, Pastaza, Ecuador; elev. 1,100 ft.

TABLE 3. Data on *Nectocaecilia ladigesi* (measurements in mm).

Museum	ZSZM	USNM	UMMZ	UMMZ
	Type			
Number	1925-245	154085	129649	129912
Locality	Rio Moju, Pará, Brasil	Utinga, Pará, Brasil	?	?
Total length	416	389	419	174
Width of body	9.5	14	10	8
Width of head	13	12	13.5	8
Height of body	17	18.5	15.7	11
Width in length approx.	43.8	28	42	21.7
Height in length	25.6	21.5	26.7	15
Primary folds	82	82	84	81
Secondary folds	0	0	0	0
Vertebrae	97	92	?	?
Premax-max teeth	19-1-20	20-1-24	23-1-22	—
Prevom-pal teeth	20-1-20	20-1-20	21-1-21	—
Dentary teeth	17-16	19-18	18-18	—
Splenial teeth	5-5	6-7	6-6	—
Sex	?	?	♀	yg

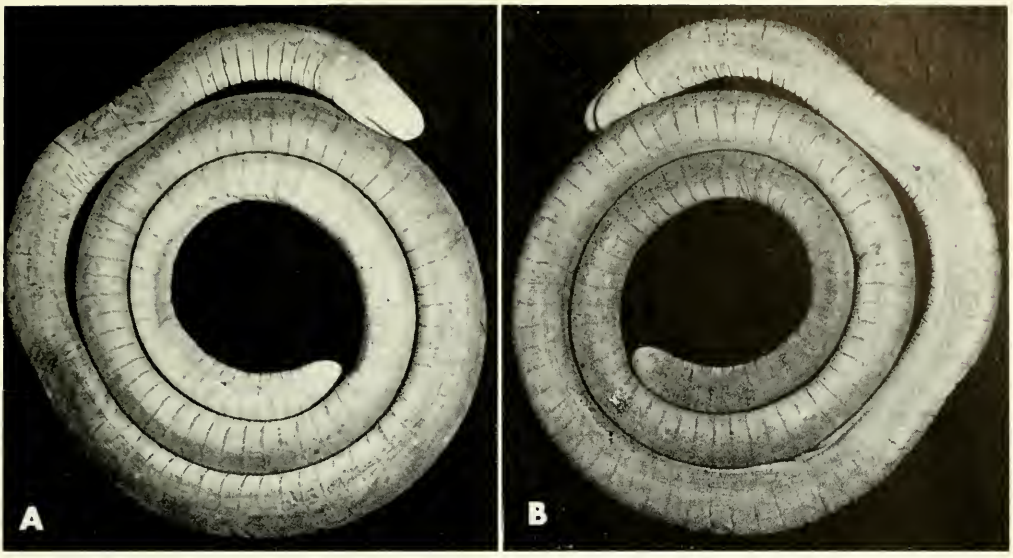

Fig. 12. *Caecilia abitaguae* Dunn. KUMNH No. 146973. Morena-Santiago Province, Ecuador. Length, 990 mm. **A,** Anterior body dorsal, subterminal part ventral; **B,** anterior part ventral, subterminal part dorsal.

Two specimens of this species have been recently taken. One is a male, KUMNH No. 119403, taken by John Lynch about 8 km NW of Mera, 1,300 m elevation, Pastaza, near the type-locality, "crawling at dusk in a ditch." It is not yet half-grown, the length being 432 mm (adults reach more than 1¼ meters in length).

The following data are available (measurements in mm): Body width, 9.7; head width, 11; tentacle from eye, 4.8; tentacle from nostril, 2; eye from nostril, 4.3; snout tip to first nuchal groove, 12.6; to second, 14.9; to third, 19.4. Primary folds, 141; no secondaries; eye in socket; nostrils well visible from above; scales begin about the 50th fold; premaxillary-maxillary teeth,

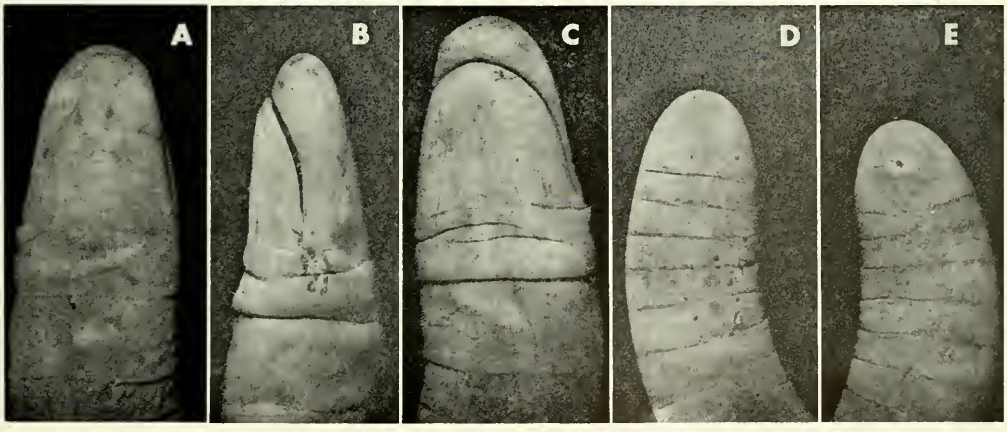

Fig. 13. *Caecilia abitaguae* Dunn. KUMNH No. 146973. Morena-Santiago Province, Ecuador. **A,** Head, dorsal view; **B,** head, lateral view; **C,** head, ventral view; **D,** terminal region, dorsal view; **E,** subterminal area, ventral view.

10-1-10; prevomeropalatine, 19-1-18; dentary, 9-10; splenial, 2-2(±); choanae small; a well-defined terminal "shield."

This specimen differs from the type in the absence of secondaries. However certain other members of the genus have a tendency to have the secondaries absent in occasional specimens. (The known specimens have only 3 and 5 secondaries.) The replacement teeth are on the point of piercing the gums so that a complete set of teeth is present. The alternative anterior teeth are presumably lost later.

The specimen in life was "blue black." Now it is slate with violet shades in certain lights. There is a small light spot at the tentacle and a small one on the area about the vent.

The second specimen, KUMNH No. 146973, recently captured by J. E. Simmons, "Río Piuntze," Cordillera del Condor, elev. 1,280 m, Morena-Santiago, Ecuador, likewise lacks a trace of secondaries. I describe it in some detail, since it appears to show some geographical variation.

Description of KUMNH No. 146973: Head relatively slender, the length 990 mm; the snout extends beyond mouth 5 mm; eye visible, the diameter of eye about 0.42 mm, in a socket; nostrils visible from directly above head; tentacular area elevated, below and slightly behind eye level, the distance from nostril, 3.4 mm, from eye, 10.2 mm, from lip, 2.5 mm. Tentacular aperture horseshoe-shaped, the end of the tentacle rounded. Snout tip to first nuchal groove, 26.5 mm; to second groove, 30.4 mm; to third groove, 39.5 mm. First collar with a transverse groove, moderately distinct above and laterally, completely delineated from second collar; second collar clearly defined above with two transverse grooves, the anterior the shorter.

Primary grooves (folds) 144, no secondary grooves. Most primaries incomplete above, dimly complete ventrally; a terminal unsegmented shield about 17 mm in length (dorsal measurement), the width near terminus, 5 mm. Anal area small, with about 5 denticulations preceding vent,

TABLE 4. Data on *Caecilia abitaguae* (measurements in mm).

Museum	UMMZ	UMMZ	CAS	KUMNH 119403	KUMNH
Number	89930	89929	5061	near Abitagua,	146973
Locality	Abitagua, Eastern Ecuador	same	same	Pastaza prov., Ecuador	Morena-Santiago, Ecuador
Total length	787	1303	303	432	990
Body width	18.8	22.1	8	9.7	20
Width in length	43.7	58.9	43	44.2	49.3
Primary folds	143	148	137	141	146
Secondary folds	3	5	5	0	0
Complete secondaries	0	0	0	0	0
Premax-max teeth	11-1-11	12-1-12	10-1-10	10-1-10	12-1-12
Prevom-pal teeth	10-1-10	12-1-12	9-1-9	9-1-8	12-1-12
Dentary teeth	10-10	13-13	10-10	9-10	11-11
Splenial teeth	3-3	4-4±	2-2	1-2	3-3
Scales begin in fold	40 to 50	50	50-60	50-60	?
Scale rows in terminal folds	1	1	1	1	1
Subdermals	none found	0	0	0	0
Sex	♂	♀	♀	♂	?
Group replacement of teeth	yes	yes	yes	yes	yes
Elevation, m.	1,100	—	—	1,300±	1,280
Vertebrae	—	—	—	142	150

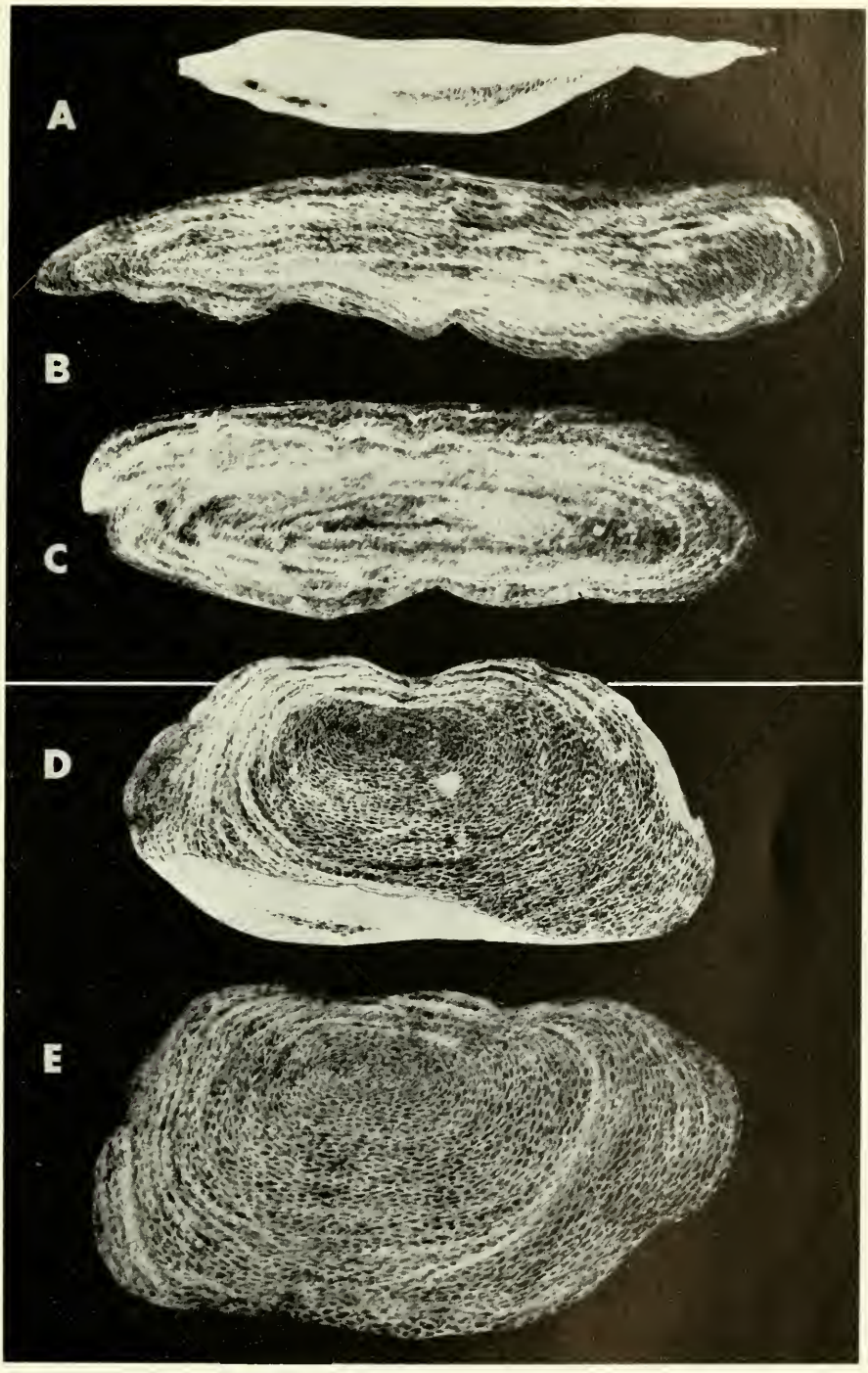

Fig. 14. *Caecilia abitaguae* Dunn. KUMNH No. 146973. Morena-Santiago Province, Ecuador. Scales: **A,** from about the 60th fold (folded); **B,** from about 80th fold; **C,** from about 90th fold; **D,** from last cm of body; **E,** from last cm of body. All scales are to the same magnification.

and about the same number behind with one larger lateral denticulation on each side; no anal glands discernible (probably female).

Scales begin about 15th fold; at first scales very small, transversely widened, their width about 0.25 mm. Over much of the body the scales form only one row in a fold, the scales four to five times wider than long. In posterior folds a single scale row, each scale in a well-defined pocket, the larger scales wider than long (2 x 2.3 mm), the "lines of growth" strongly marked. The folds are difficult to separate from their posterior attachment.

Tongue free anteriorly with two small teatlike narial plugs somewhat back from the anterior edge; internal nares moderate in size, the diameter of one in the distance between them about twice. The vertebrae number 150.

Dentition: Group loss and group replacement of premaxillary-maxillary series (anterior teeth) 11-1-11, the 1, 3, 5, teeth functional, the alternate teeth about ready to erupt; maxillary teeth, 6, much smaller,

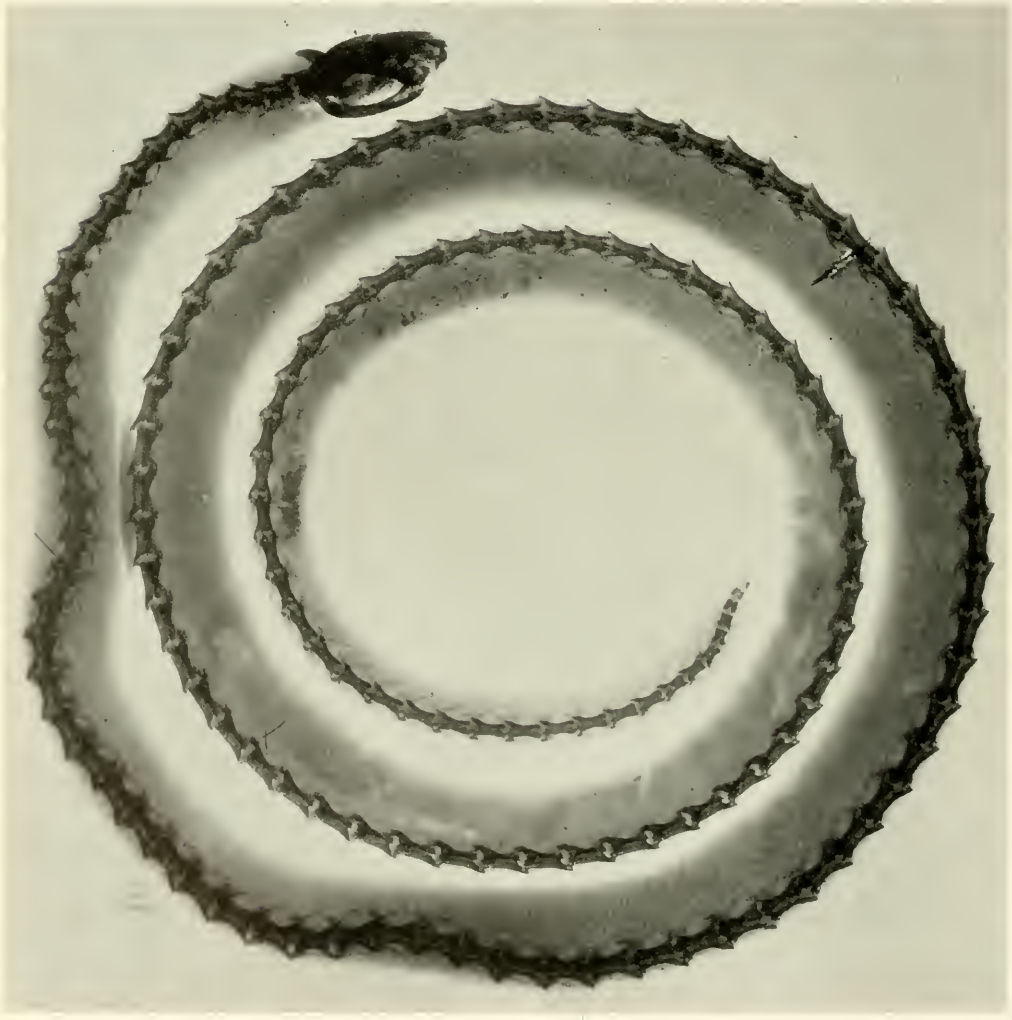

FIG. 15. *Caecilia abitaguae* Dunn. KUMNH No. 146973. Morena-Santiago Province, Ecuador. X-ray, vertebrae, 150. Length, 990 mm.

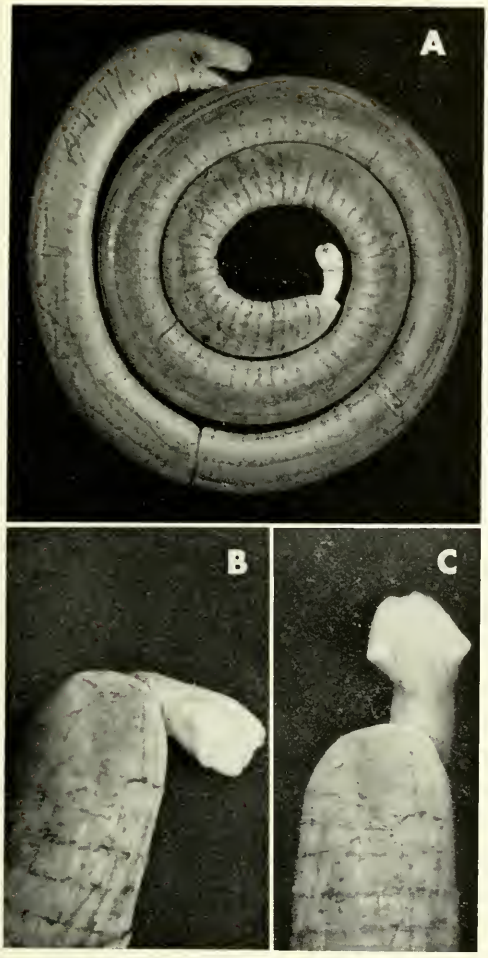

Fig. 16. *Caecilia abitaguae* Dunn. KUMNH No. 119403. Near Abitagua, Pastaza Province, Ecuador. **A,** Lateral view of body showing extruded penis; **B,** lateral view of penis, enlarged; **C,** dorsal view of same, enlarged. Length of body, 432 mm.

all functional; prevomeropalatine series, 12-1-12, with prevomers 1, 3, 5 functional, and larger than the seven palatine teeth; dentary teeth, anterior functional and very large proportionally, the posterior teeth very small. Splenials deeply buried in tissue, 2-2. The two series in the upper jaw rather widely separated and definitely not parallel.

Color: Body blackish gray on dorsum. Lower half of sides a lighter gray with dim dark borders on edge of folds. Head lighter gray than body, the color extending back somewhat on neck, especially so on ventral part. No light spots at eyes or nostrils; area about tentacle vaguely pinkish as is the region about vent.

Measurements in mm: Total length, 990; width of head, 20; width of neck, 22; body width, about 20; the width in length, about 45.4 times.

The relationship of this form is with certain other described forms of the genus but they differ as follows:

C. caribea: This has about the same number of primary folds, 142-151 (144). The most striking difference is the complete absence of scales on the body.

C. corpulenta: This species has a wide yellow stripe, and lacks scales completely (both scales in grooves and subdermals); subterminal region white or yellow. Primary folds, 123; no secondaries.

C. crassisquama: Primary folds, 174; a yellowish olive lateral stripe not clearly defined; scales present only in five or six most posterior folds, the scales thick, inflexible, unable to be flattened; no subdermals.

C. occidentalis: A narrow yellowish stripe present; primaries, 218; width in length, 111 times.

C. attenuata: No scales in folds; no subdermal scales (except one specimen has a few scales in last five folds). Primary folds, 182-191; width in length, 62-87 times.

C. antioquiaensis: Primary folds, about 171, with two or three scale rows in each posterior fold. Subdermal folds present.

C. abitaguae: Primary folds, 143-148; reaching a length of 1,300 mm. Some specimens have a very few secondaries while others have none.

Caecilia attenuata Taylor

(Figs. 17-18)

Caecilia attenuata Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 358-359. Type-locality, "Peru."

This species was described from two somewhat desiccated young specimens from Perú without definite locality. A recent specimen, KUMNH No. 143556, was collected by Bruce MacBryde 10.4 km N of Santa Rosa, in Napo, Ecuador, at an elevation of 1,910 meters. The specimen, splendidly preserved, measures 910 mm in length, the head width (greatest) 12 mm, the width of body (about) 10.4 mm. Tentacle to eye, 8 mm; tentacle to nostril, 2.3 mm. Snout tip to 1st groove, 18.4 mm; to second groove, 21.3 mm; to third groove, 27.5 mm. Snout projects beyond mouth 3 mm.

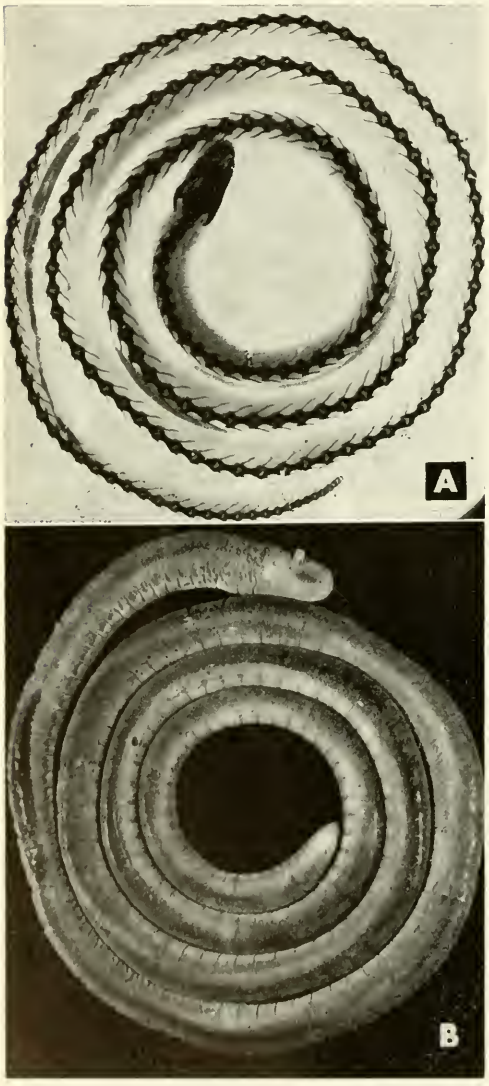

FIG. 17. *Caecilia attenuata* Taylor. KUMNH No. 143556. Napo Province, Ecuador, elev. 1910 m. A, X-ray, vertebrae, 191; B, dorso-dorsolateral view of body. Length, 910 mm.

The primary folds are 182 followed by an unsegmented "shield" measuring (dorsally) 8 mm in length. No secondaries. The folds are incomplete above, except the last 15, but in the ventral region all are complete.

The eye is small, in a socket, slightly raised, barely visible externally. Nostrils plainly visible from directly above head. The tentacular aperture, not visible from above, is 2.3 mm distant from nostril and almost directly below it; the distance from eye, 8 mm. The vent is small as is the whitish surrounding area. Subterminally there is a deep-black flat depression.

The choanae are small, the distance between them about 1.4 mm, each about 1 mm in diameter. The palate is striated and the tongue relatively short with two teatlike narial plugs near the front border.

The premaxillary-maxillary teeth show group-loss and group-replacement. There are 8-1-8 teeth in the full set but only the alternate teeth 2, 4, 6 are functioning while the numbers 1, 3, 5 are nearly ready to erupt. In the prevomeropalatine series, of 8-1-8, the same is true. Dentary teeth are 10-9, the alternate teeth on each side functioning, the missing teeth ready to erupt.

The splenials are 2-2 but at a much lower level than the dentary series. The gums appear to be much swollen and the palatine and splenial teeth are deeply sunk in the gums.

Both nuchal collars have a transverse groove and the second is fused below to the first primary fold.

Scales are present in the last five folds, but only three or four scales are present on each side of the fold and the scales are not overlapping. I found no subdermal scales. Seemingly the elongate skin glandules usually present in folds above the scales in

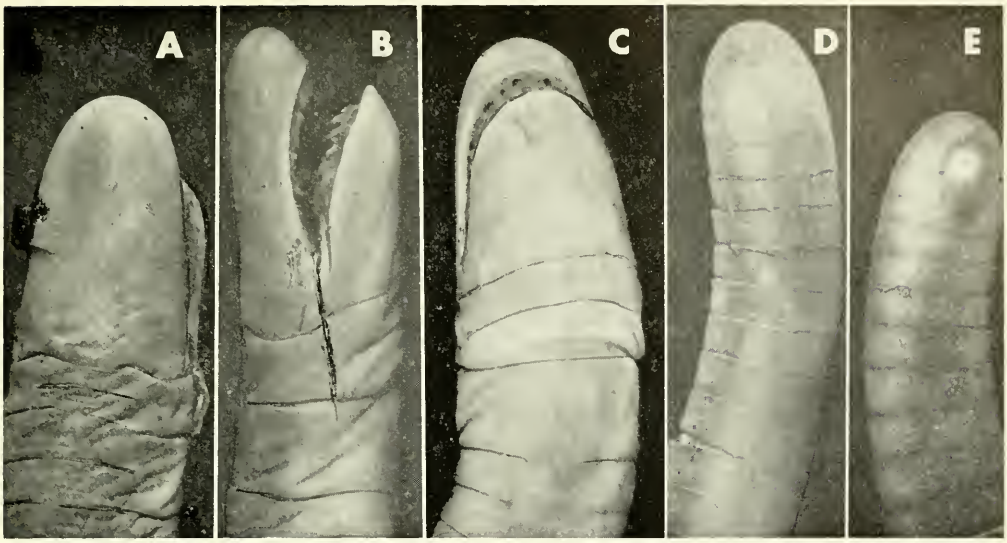

Fig. 18. *Caecilia attenuata* Taylor. KUMNH No. 143556. Napo Province, Ecuador. **A,** Head, dorsal view; **B,** head and neck, lateral view; **C,** head and neck, ventral view; **D,** posterior body, dorsal view; **E,** subterminal part of body, ventral view.

caecilians of this genus are absent or greatly reduced in length.

The color generally is blackish above. There is a light ventrolateral area (stripe), which anteriorly, for about 15 cm, shows a distinctly pinkish coloration, and is broken by vertical black lines on the edge of the folds. Farther back the area becomes more greyish and the pinkish coloration all but disappears. The sides of the head and snout-tip are slightly lighter as are areas about eyes, nostrils, tentacles, and the immediate region of the vent.

Compared with the two types, in which body width in length is 62-66 times, it will be noted that in this specimen, more than twice as large as either type, the width in length is approximately 87 times.

There are color differences. The type is brownish presumably due to its having been in the preserving fluid many years. Scales were stated not to be present in the types but some actually may be present and were not found by me. The older specimen shows the ventral part of the folds generally complete. No secondaries are present. Vertebrae, 190. The number of primaries, 182, extends variation formerly reported 189-192. The dentition in the three specimens is very similar.

Caecilia bokermanni Taylor

Caecilia bokermanni Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 359-363, figs. 188-190.

A second specimen of *bokermanni* is also from the type-locality, Río Bobonaza, Chicherota, Napo-Pastaza, Ecuador.

The following measurements (in mm) are from this specimen: total length, 333; width of head, 5.2; body width, 5; body height, 6.7; tentacle to eye, 2.6; tentacle to nostril, 1; snout tip to 1st groove, 86; to 2nd groove, 10.7; to 3rd groove, 13; snout projects 1.7.

The primary folds are 192, incomplete above except in the posterior part of body; secondary folds 14, of which 4 are complete.

Eye in a socket, skin covered, and now not visible externally; both nostrils visible from directly above; choanae large, the diameter of one a little narrower than the interchoanal distance; tongue practically

destroyed; vent nearly circular. Group-loss and group-replacement of teeth. Premaxillary-maxillary teeth, 9-9; prevomeropalatine, 8-9; dentaries with tissues removed and destroyed; splenials 2-2.

Scales begin near first secondaries; one scale row present in folds of last two centimeters. No subdermal scales discovered. Specimen presumably a young male. The terminal shield small. No light spots on head or vent.

The specimen is now uniformly brownish, the head not obviously lighter than the body.

Caecilia corpulenta Taylor

Caecilia corpulenta Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 365-369, figs. 191-193.

On page 369, Taylor, as a result of a lapsus, compared this form with what he calls *Caecilia haydee* Roze. There is no such species. *Caecilia flavomaculata* Roze and Solano was intended; *haydee* (Roze) is a species of *Nectocaecilia*.

Caecilia disossea Taylor

The type of this species is AMNH No. 42832 from the mouth of the Río Santiago, Perú. It was listed by Dunn (1942) as a paratype of *Caecilia bassleri* Dunn, but differs from *bassleri* in having an eye socket, the eye not covered by bone.

I have recently had five specimens from Lago Agrio, Napo, Ecuador for examination. These are KUMNH Nos. 34902, 35251, 125314, 125315 and 125330. The counts of the primary folds are within the range 238-262; the secondaries, 34-39.

Dunn (1942) gives the number of primary folds on a second paratype, AMNH No. 42852, as 285; the secondaries as 17. These counts have not been verified. Since the primary count is much outside the known variational limits, it may be questioned.

Caecilia dunni Hershkovitz

Hershkovitz (1938) described *Caecilia dunni* from a single specimen obtained near Tena, Napo-Pastaza, Ecuador at an elevation of 1,700 ft. (Atlantic drainage).

Characteristic of the species the author records 124 primary folds (including the two collars) and 68 secondary folds, 5 of which are complete. The length was 455 mm, the body diameter 13 mm, the head width 9.5 mm.

The dorsal surface is blue, the ventral surface paler with grayish mottling. The body is cylindrical and fairly thick (stout) throughout.

The author regards it closely related to *Caecilia tentaculata*!

Dunn's treatment in his 1942 paper associated with this form not only the type specimen but some 18 other specimens, one from NW Ecuador (probably Pacific drainage) and 17 from the Atrato and Chocó region of Colombia. Among these are two specimens described by Boulenger (1913) as *Caecilia intermedia* (while several other cotypes of *Caecilia intermedia* were referred to *Caecilia nigricans* Boulenger!).

Dunn himself was not satisfied with this arrangement and states "with more material the form might be divided." He suggests four possible divisions. It seems that most of these forms from the Pacific or Carribean drainage systems should be referred to *Caecilia perdita*, but this will necessitate a re-examination of the specimens so treated.

Caecilia inca sp. nov.

(Figs. 19-21)

HOLOTYPE: USNM No. 119008 ♂ from "Fundo Sinchona," Loreta, Perú. Collected by J. G. Sanders, July, 1944.

DIAGNOSIS: A large species, moderately slender, elongate (1,069 mm), with a body width about 16 mm. Primary folds 158, incomplete; no secondary folds present.

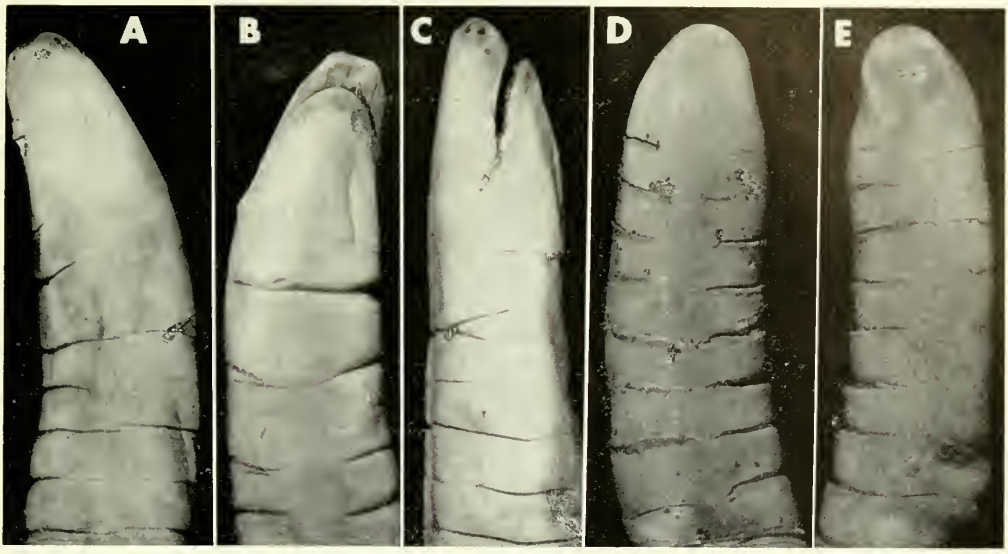

Fig. 19. *Caecilia inca* sp. nov. Type. USNM No. 119008 ♂. "Fundo Sinchona," Loreta, Perú. **A,** Head and neck, dorsal view; **B,** head and neck, ventral view; **C,** head and neck, lateral view; **D,** posterior body, dorsal view; **E,** posterior body, ventral view.

Width in length about 66 times. Scales begin at about the 10th fold with two or three scales on each side of the fold. The number of scales increases but there is a maximum of only one row of scales in each fold, with occasional extra scales. No evidence was found of group-loss and group-replacement of teeth. Eye in socket slightly visible externally. Color, grayish slate with a vague wash ventrolaterally of yellowish olive.

Description of the Holotype: Head somewhat narrowed towards the rounded snout tip, its greatest width 12.5 mm, its length from the snout-tip to back of second collar, 27 mm. Eye in a socket, dimly indicated externally and slightly raised. Tentacular aperture directly below nostril, 2.5 mm from the nostril, 7 mm from the eye, not visible from directly above the head. Nostrils small, distinctly visible from above the head; snout projects beyond mouth 3.8 mm.

The primary folds 158, incomplete both above and below except for 2 or 3 terminal ones. No secondaries present. An unsegmented terminal "shield." No tail. The depressed vent area measures 4 x 3 mm with numerous short denticulations preceding and following vent. Two anal glands visible on lateral denticles preceding the vent. The terminus of the body is slightly wider than the head.

Scales begin to appear in the 10th fold and a little farther back there is one scale row as long as the two sides of the fold. This number continues to the terminus of the body although there may be some few scattered extra scales. In the two or three complete terminal folds the rows may completely surround the body. The individual scales are encased in nearly transparent thin tissue pockets. The largest scales measure about 2.3 x 3.3 mm.

Dentition: There is no direct evidence that the anterior teeth are lost and replaced in groups. However, as has already been reported, even in species where this occurs, there is one time in the cycle when the replaced tooth group may be functioning before the other group is lost. This being the case one cannot be certain. The tooth formulae are: premaxillary-maxillary, 10-1-10; prevomeropalatine, 10-1-11; dentary,

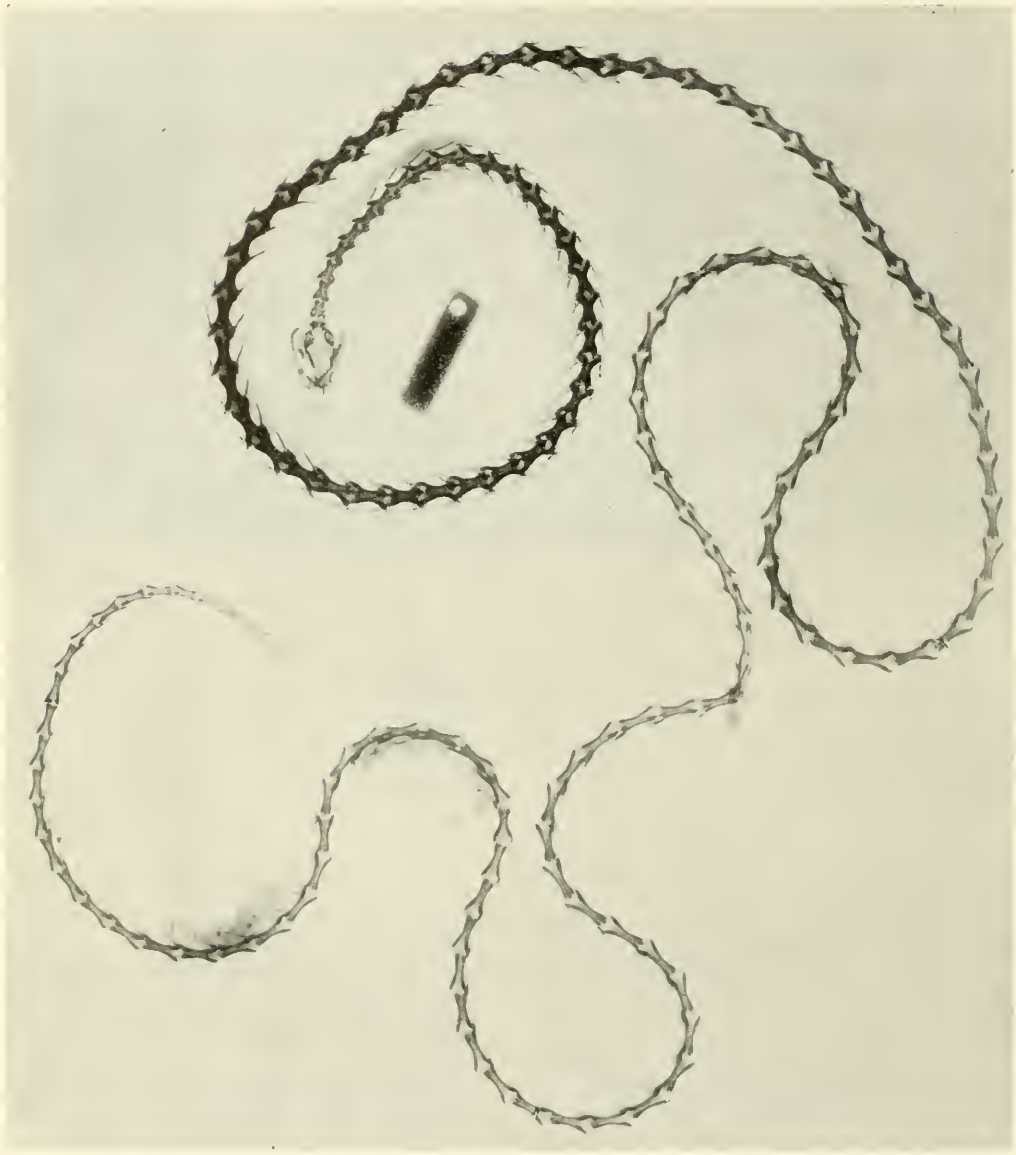

FIG. 20 *Caecilia inca* sp. nov. Type. USNM No. 119008 ♂. X-ray. Length, 1,069 mm; vertebrae, 158. (Note larger anterior vertebrae, and smaller ones in latter four-fifths of the body.)

10-10; splenial, 2-2. The premaxillary teeth are about double the size of the prevomerine teeth, the anterior dentary teeth being largest of all. The splenials are minute.

The tongue has two well-developed narial plugs that in this specimen extend forward slightly in advance of the tip of the tongue. The choanae are relatively small, the diameter of one is contained in the distance between them about 2.7 times.

Measurements in mm: Total length, 1,069; width of head, 12.5; width of body, 16; snout projects 3.8; width in length about 66 times.

REMARKS: In "Caecilians of the World," figures 226 and 227 were unintentionally included as illustrations of

Caecilia pachynema. They are actually illustrations of this new species, *C. inca*. Drawings had been made of this by my artist who labeled the drawing with the data attached to it. I had concluded that the specimen did not belong to the species

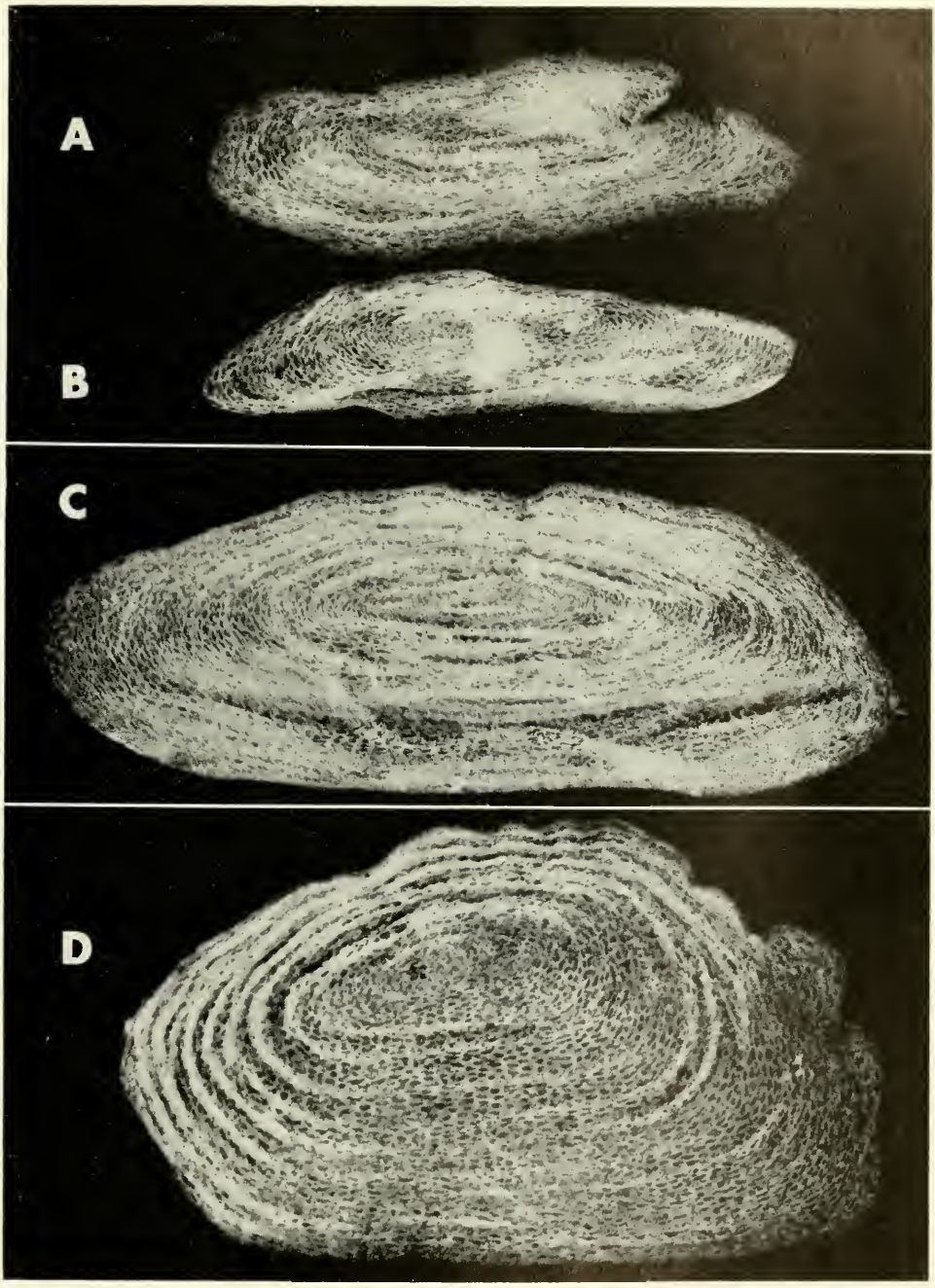

Fig. 21. *Caecilia inca* sp. nov. Type. USNM No. 119008 ♂. "Fundo Sinchona," Loreta, Perú. Scales: **A-B**, from about 25th fold; **C**, from 2 cm from end of body; **D**, from last cm of body. Largest scale about 2.3 x 3.3 mm; all scales are to the same magnification. (Note strongly marked concentric lines of growth.)

C. pachynema as it was labeled and withdrew it from the work. I could not associate it with any other described species. Through some error during the editing of the work these two figures were reinstated without my knowledge. However, in the text I state that I have not examined Peruvian specimens of the species.

After reexamination of much material from Colombia, Ecuador and Perú I am still unable to find a described counterpart and at last I am describing this form as presumably an undescribed species. I have been unfortunate in not finding the exact type-locality "Fundo Sinchona" in Loreto, since it is not marked on Peruvian maps available to me. This is not surprising since the name Fundo Sinchona suggests that it is a rural property, perhaps a private hacienda or rancho. Loreta is a very large State, nearly 800 miles in north-south length and about 500 miles in its widest part. It is for the most part lowland, lying in the drainage area of the upper Amazonian tributaries. The name "inca" refers to the rulers of the primitive inhabitants of Perú.

The extraordinary difference in color, color pattern, and adult size, and the fact that scales are present throughout most of the body, should separate this form without difficulty from *Caecilia pachynema* Günther.

Caecilia leucocephala Taylor
(Figs. 22-23)

This species was described from a juvenile specimen measuring 189 mm from the "Río Riposo," Valle del Cauca, Colombia. Two other specimens have become available and data from these are compared with those from the type. The first, CAS No. 66187, is said to be an exchange specimen from Dr. F. Werner, Wien, Austria, originating in "Central Brasil." It was originally labelled *C. pachynema*. The specimen has become stiffened and its present length is estimated. The terminus of the body has a small whitish area.

The second specimen is KUMNH No. 94378, from Cana, Darién, Panamá. The color is nearly slate black save for the whitish head and white vent area. In both specimens there is a vague darker area on each side of the occiput.

TABLE 5. Data on *Caecilia leucocephala* (measurements in mm).

Museum Number	EHT-HMS 583	CAS 66187	KUMNH 94378
Total length	189	455	306
Body width	6	11	8
Width in length, approx.	31.5	41	38
Primary folds	118	118	131
Secondary folds	42	32	54
Complete secondaries	8	9	9
Premax-max teeth	8-1-8	10-1-10	9-1-9
Prevom-pal teeth	10-1-10	9-1-8	9-1-9
Dentary teeth	11-11	11-11	11-11
Splenial teeth	2-2	2-2	3-3
Scales begin, fold (ca)	25	31	25
Scale rows in terminal folds	1	1	1
Subdermals present	yes	yes	yes

The scales of CAS No. 66187 show what appear to be concentric seasonal lines of growth. These were almost completely missing in the young type. The light color of the head is very pronounced while the head color of the type has become brownish white in preservative. The head color of the Panamá specimen also is lighter than is the type now.

The California Academy specimen purports to be from "Central Brasil," but most probably the locality is in error. It is more likely from a locality in the Pacific or Caribbean drainage.

The width of the head is greater proportionally than in the juvenile type.

Caecilia mertensi sp. nov.
(Figs. 24-26)

HOLOTYPE: CAS No. 63983, an exchange specimen purporting to come from

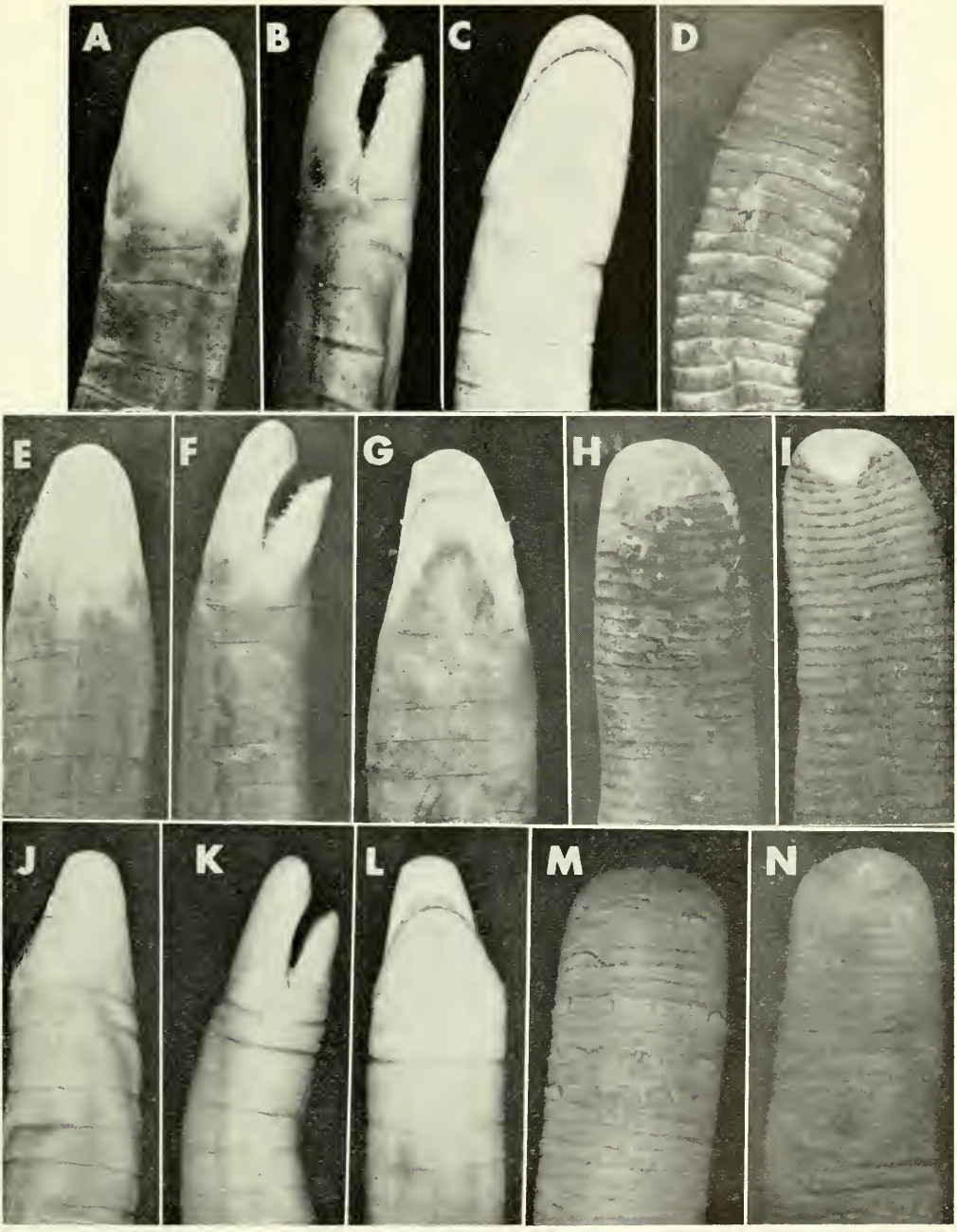

Fig 22. *Caecilia leucocephala* Taylor. **A-D**, EHT-HMS No. 583, "Río Riposa," Valle del Cauca, Colombia. Dorsal, lateral and ventral views of head, and dorsal view of terminal part of body. **E-I**, KUMNH No. 94378, Cana, Darién, Panamá. Dorsal, lateral and ventral views of head, and dorsal and ventral views of posterior body. **J-N**, CAS No. 66187, "Central Brasil." Dorsal, lateral and ventral views of head and neck, and dorsal and ventral views of posterior end of body.

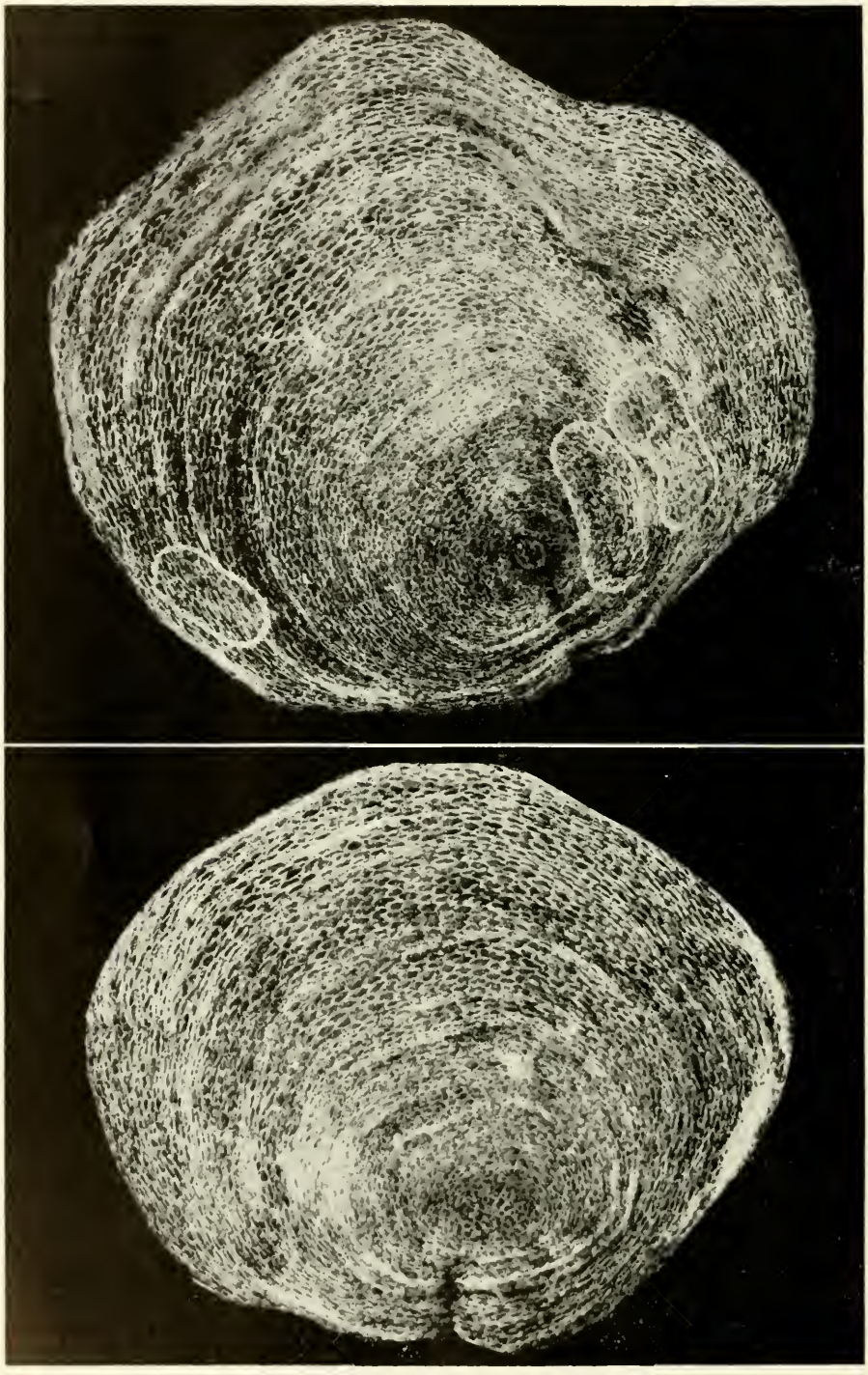

FIG. 23. *Caecilia leucocephala* Taylor. CAS No. 66187. Two scales (same magnification) from last cm of body.

"Seychelle Isle." It is most probably a specimen from South America since the genus *Caecilia* is known only from South and Central America.

Diagnosis: A moderately elongate species with a known length of 495 mm and a body width of about 12.5 mm; head width 9 mm, narrower than the terminus of the body (11 mm). Snout rounded, head not depressed. Tentacular aperture below and vaguely posterior to the nostril, but much closer to the nostril than to the eye. Primary folds, 142, incomplete above and below throughout most of the body.

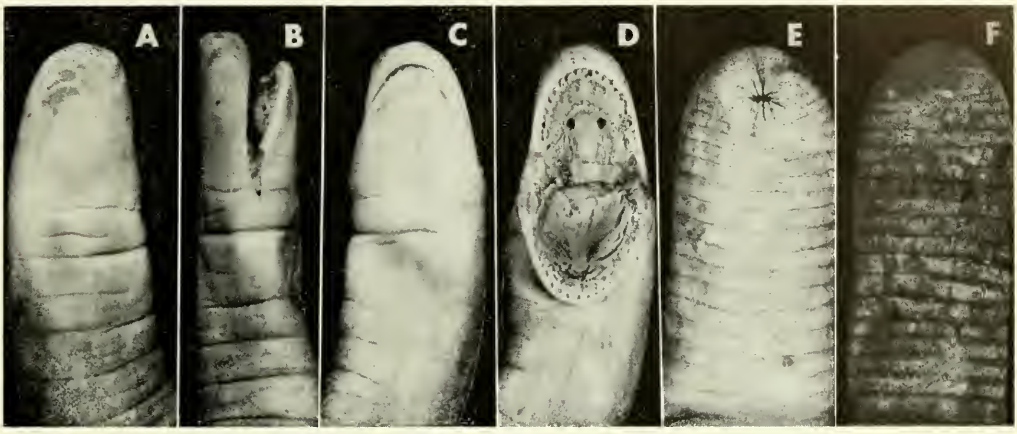

Fig. 24. *Caecilia mertensi* sp. nov. Type. CAS No. 63983. **A-C,** Dorsal, lateral and ventral views of head region; **D,** buccal area; **E-F,** ventral and dorsal views of terminal part of body.

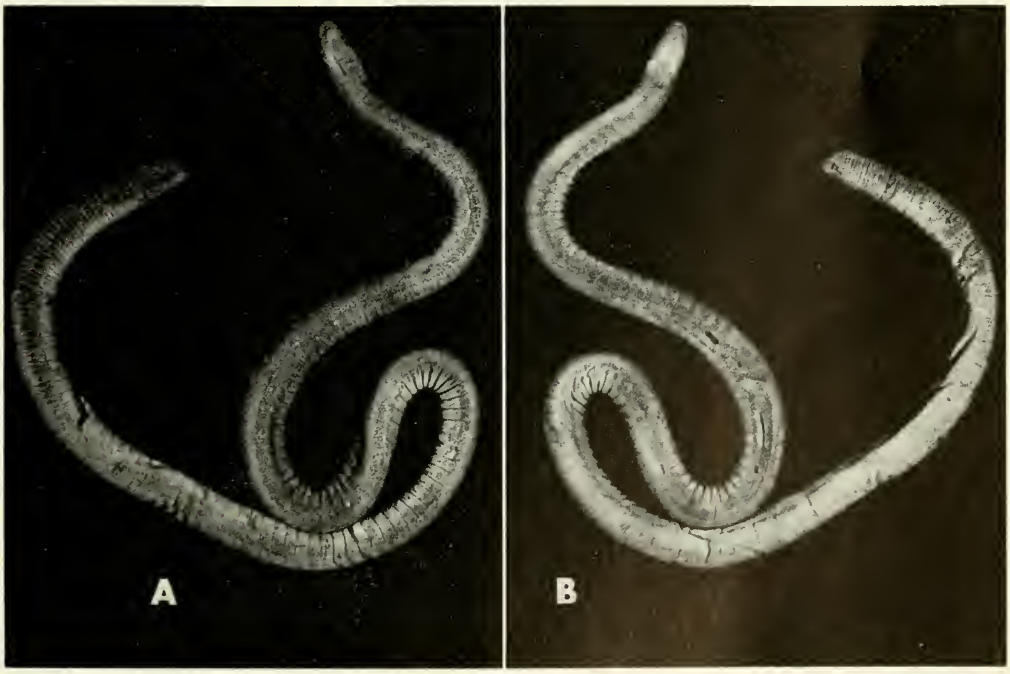

Fig. 25. *Caecilia mertensi* sp. nov. Type. CAS No. 63983. **A,** Dorsal view of body; **B,** ventral view of body. Length, 495 mm.

Secondary folds, 48, and the 12 anterior folds lateral and very short while the last 4 completely surround the body. Color grayish brown, the head and lower jaw grayish. Splenial teeth, 2-2. Only a single scale row in a fold.

DESCRIPTION OF THE HOLOTYPE: Head narrowed a little anteriorly, the snout projecting 1.6 mm; eyes very small, in a socket, visible externally. Distance from snout tip to first nuchal groove, 11 mm; to second groove, 14.2 mm; to third groove, 17.4 mm. First collar distinct dorsally, somewhat less so ventrally, with a transverse dorsal groove; second collar very distinct above, less so ventrally where it fuses with the first primary fold. A dorsal transverse groove present.

Scales begin at or near the 25th fold. These are wider than long; more posteriorly the scales increase in number in the fold and become proportionally longer, and the initium becomes proportionally nearer the anterior edge of the scale. The largest scales measure about 1.7 x 2.3 mm. The scales anteriorly are much smaller and the lines of growth are more evident.

The skin glandules are rather conspicuous. Three types may readily be distinguished. The largest are the elongate glandules seen in the folds above and below the scales, lying longitudinally. The smallest are usually about 0.10 to 0.18 mm in surface diameter. Then there are numerous glandules that measure 0.5-0.9 mm in diameter. The surface of this third type has several darker areas which give the glandule a lacelike appearance.

Dentition: The teeth appear to be smaller than in most of the species of *Caecilia*. The premaxillary-maxillary teeth, 10-1-10; prevomeropalatine, 11-1-11; dentary, 12-12; splenial, 2-2. The median part of the premaxillary series is rather widely separated from the prevomerine series (not parallel).

The tongue has two strongly developed lateral narial plugs, and the area between these plugs is pitted. The internal nares are relatively small, the diameter of one in the distance between, about 3 times.

Measurements in mm: Total length, 495; greatest head width, 9; body width, 12.5; terminal width, 11; tentacle to nostril, 1.9; tentacle to eye, 4; width in length, about 39 times.

Color: The color is a light brown, becoming grayish brown laterally; posteriorly the brown is a little more intense and the folds appear to have a dark and a grayish band. Head grayish above and below; the ventral surface of the neck and body is lighter, approaching fawn color. There is no distinct light spot at the vent; neither are there spots of white at the eye and nostril.

REMARKS: Despite the attached data, I feel certain that the specimen originated in South America rather than in the Seychelles. There is no certain clue as to exactly where it may have originated. I would place it in the Eastern Atlantic drainage.

Caecilia nigricans Boulenger
(Fig. 27)

This large species seemingly is confined to the Pacific drainage of Ecuador, Colombia and eastern Panamá. Thanks to Dr. John Wright, I have recently examined two specimens from the LACMNH collection.

The first, No. 72741, is from the north slope of Alto del Buey, between 420 and 500 ft. elevation, Chocó, Colombia. The length is 555 mm, the primary folds, 184, the secondaries, 58. Scales begin about the 33rd fold with a single row continuing in each fold to the terminus and with numerous scattered scales forming partial additional rows.

The second specimen is No. 72742. The length is 476 mm; the body width, 7.2 mm; the height of body, 11 mm; width of

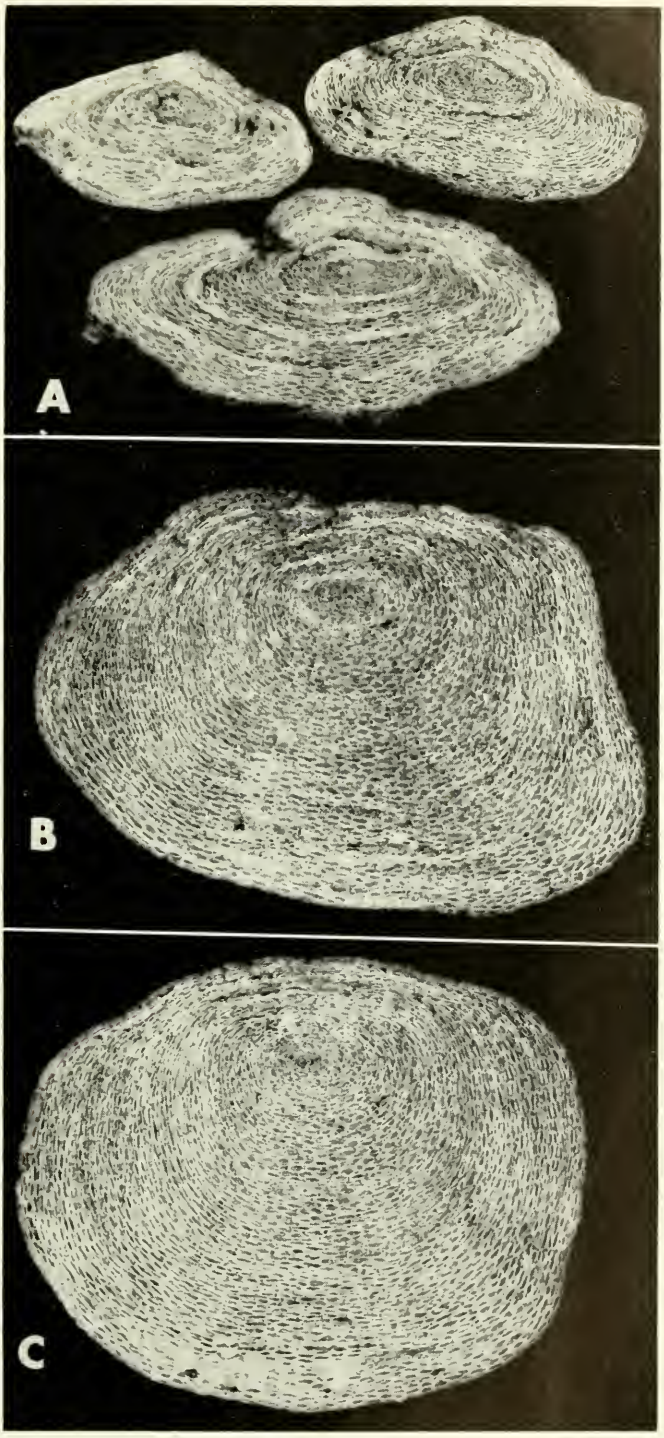

Fig. 26. *Caecilia mertensi* sp. nov. Type. CAS No. 63983. Scales: **A**, from about 50th fold; **B-C**, from last cm of body. All scales are to the same magnification.

head, 9.3 mm. The terminus is 9 mm wide and 10 mm high. The primary folds are 163, incomplete both above and below except on the posterior part of the body. Secondary folds are 45, of which five are complete. Scales begin at about the 38th

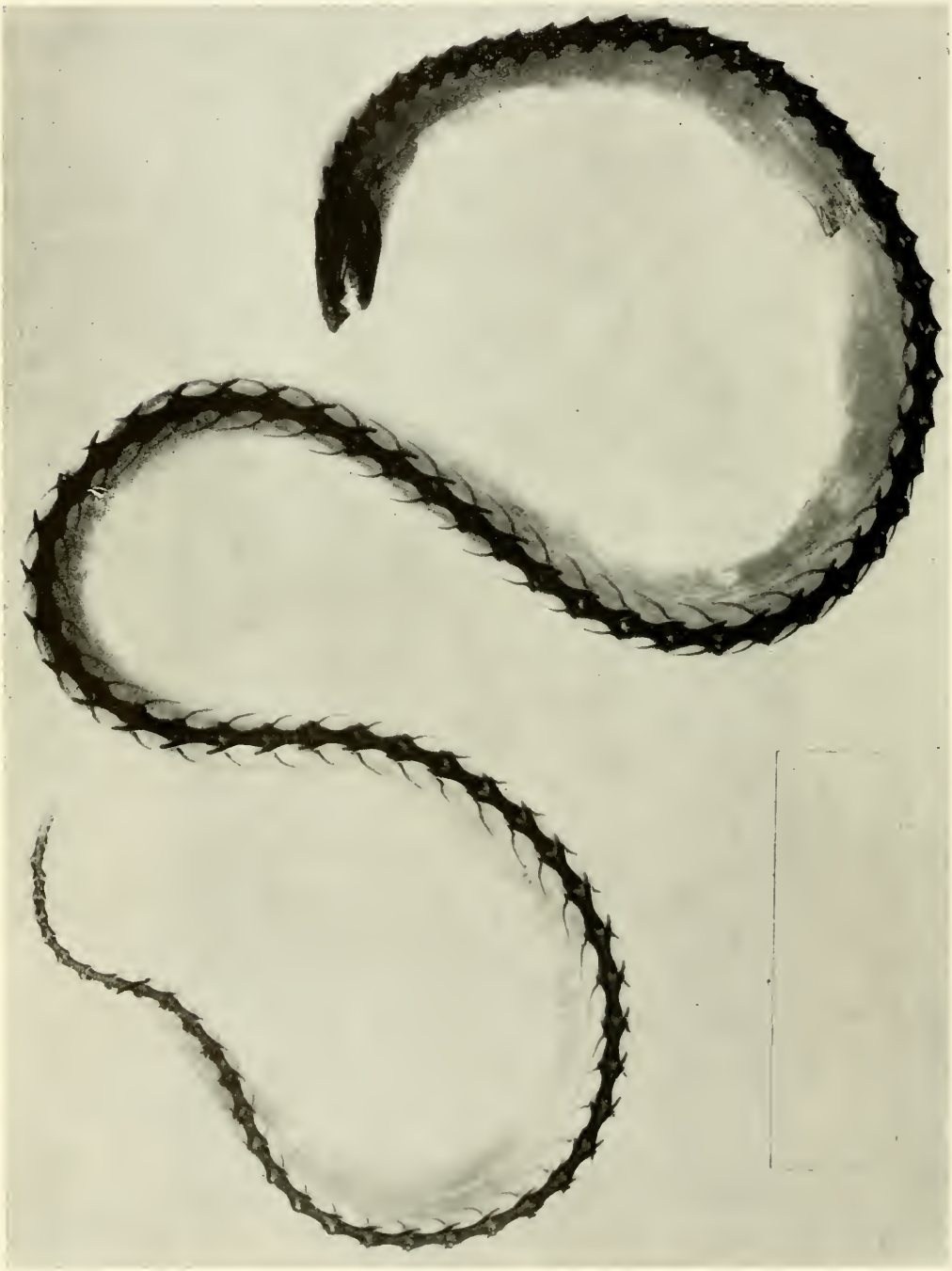

FIG. 27. *Caecilia nigricans* Boulenger. LACMNH No. 72742. Chocó, Colombia. X-ray. Length, 476 mm.

primary fold, and in the latter part of the body there are three scale rows in each fold, one larger than the other two. Scales of the largest row measure about 3 x 3 mm. Subdermal scales are present.

The range of variation of the number of primary folds of this species tends to exceed the usual limitations. Based on my counts and those in the literature the range is 156 to 192. However, the low number is of the synonymized *C. intermedia,* and the high number, from AMNH No. 90377, should be verified.

A caecilian living on Gorgona Island, an island about 40 km off-shore from southern Colombia, is referred to this species since it obviously derived from *nigricans* but not greatly changed. Its primaries are 164, its secondaries 36, three of which are complete.

Caecilia perdita Taylor
(Figs. 28-30)

Caecilia perdita Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 309-404, figs. 208-211. Type-locality, Andagoya, Condoto, Chocó, Colombia.

This species is known only from the Pacific slope of western Colombia. A recently collected specimen, CAS No. 119586, is from "Caño Discordo, between Cucurrupi and Noanama, on Río San Juan," collected by B. Malkin. The specimen agrees in essential detail with other known specimens. The primary folds are 139, the secondaries 80. The known range for the primaries is 133-152; for the secondaries 64-83. The terminal folds have a single row of relatively large scales.

Figures 28 and 29 show the considerable widening of the terminal part of the body and the slenderness of the head. The characteristics of the skin glands of the terminal parts are clearly shown in Figure 29. The character of scales from the terminal centimeter is shown in Figure 30. It would appear that the specimens occurring in the Pacific drainage area referred by Dr. Dunn (1942) to the species *C. dunni* may belong to this species.

Caecilia tentaculata Linnaeus
(Fig. 31)

Although this Linnaean name has been applied to the species to which these data

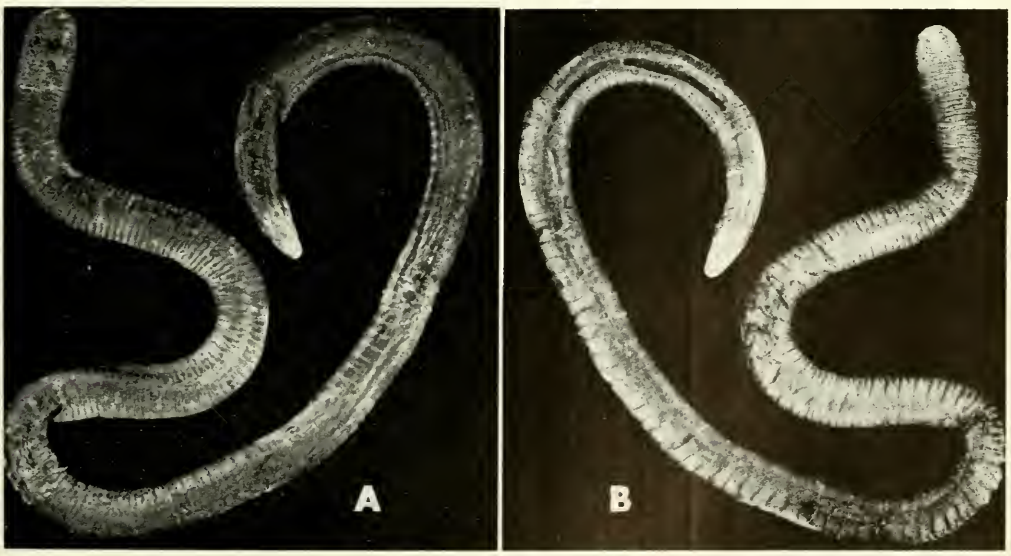

Fig. 28. *Caecilia perdita* Taylor. CAS No. 119586. Caño Discordo, Río San Juan, Colombia. **A,** Dorsal surface; **B,** ventral surface.

TABLE 6. Data on *Caecilia tentaculata* from Santa Caecilia, Napo, Ecuador (measurements in mm).

Number (KUMNH)	35683	98518	125318	125319	125320 ♂	125321 ♂	125322	125323	104434	104435	104436 ♂	104437 ♂	104438	104439 ♂	119392	119394 ♂
Total length	582	490	324	399	638	712	583	606	770	805	780+	710	800	850±	612	602±
Head width	19	13.4	9.7	11	16	19	17	22	20	21	19	19	21	23	16	16
Body width	22.2	15.2	9.8	12.8	24.2	28	21.8	28	33	32	29	24	31.5	32	17.5	20
Body width in length	26	32	32	31	26	25	26.7	21.6	23.3	22	27	29.5	24.6	26.5	35	30
Snout projects	4.2	3.7	2.7	2.4	4.6	4.9	4.5	4.2	4.5	6	5	6.2	6	6	4+	4+
Tentacle to eye	8.4	7	4.2	5	8.6	9.4	9.1	9.9	10	9	10	9	10	9	8	7.8
Tentacle to nostril	1.9	2.7	2	2.5	3.9	4.1	4.2	4	4.2	4	4.2	3.7	4.5	4.2	2.3	2
Snout tip to 1st groove	23	15.8	11	14.6	20	—	20	23	22	23	23	22.5	25	25	22.5	?
Snout tip to 2nd groove	26.8	20.2	13.7	17.3	24.7	28	25.6	28	30	29.2	30	27	33	34	27	?
Snout tip to 3rd groove	33.8	28	17.6	22	32.8	35	32	36	37±	40	38	37	41	42	36	?
Primary folds	121	119	121	119	118	119	118	116	115	119	122	119	119	119	121	122
Secondary folds	33	23	43	45	31	50±	36	44	40	34	37	34	34	32	38	45
Complete secondaries	4 or 5	0	5	4	3	3	?	3	6	3 or 4	4 or 5	3	4	4	4 or 5	5
Premax-max teeth	8-1-8	11-1-11	11-1-11	9-1-9	10-1-10	?	11-1-11	9-1-9	10-1-10	10-1-10	12-1-14	10-1-11	12-1-12	12-1-12	13-1-13	?
Prevom-pal teeth	9-1-9	11-1-11	10-1-10	10-1-9	12-1-12	?	10-1-11	12-1-12	11-1-10	13-1-14	13-1-13	13-1-12	14-1-15	15-1-15	11-1-11	?
Dentary teeth	8-8	10-10	10-10	11-11	9-9	?	12-12	10-10	10-10	13-13	12-12	12-12	13-13	13-13	10-10	?
Splenial teeth	1-2	3-?	2-2	2-2	3-3	?	3-3	2-2	2-2	3-3	3-3	3-2?	3-3	1-2?	1-2	?
Eye small in socket	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes

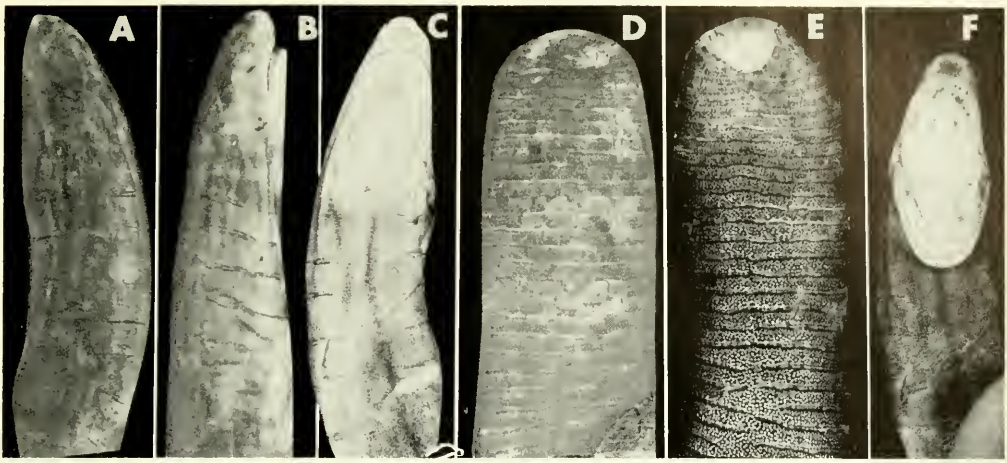

Fig. 29. *Caecilia perdita* Taylor. CAS No. 119586. Caño Discordo, Río San Juan, Colombia. **A-C,** Dorsal, lateral and ventral views of the head; **D-E,** dorsal and ventral views of the terminal part of the body; **F,** buccal region.

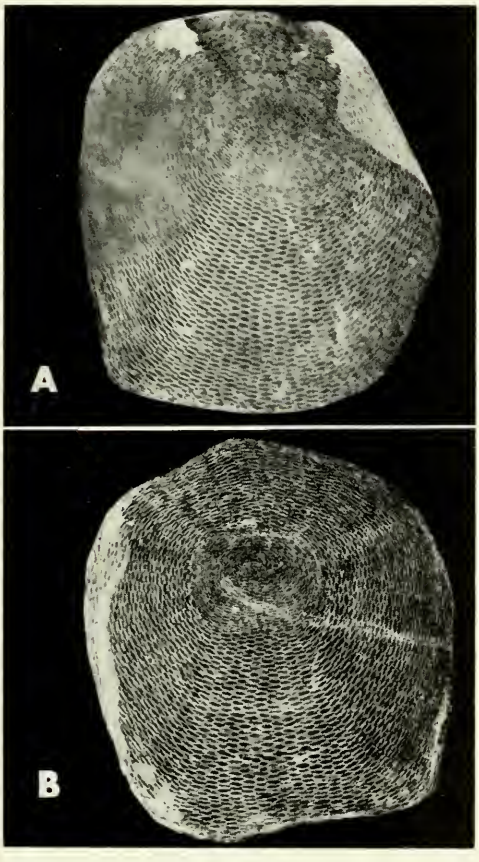

Fig. 30. *Caecilia perdita* Taylor. CAS No. 119586. Caño Discordo, Río San Juan, Colombia. Two scales (same magnification) from last cm of body. Size of B scale, 1.1 x 1.6 mm.

apply, there is considerable doubt that such an association is correct. Elsewhere I am presenting evidence that it is incorrect, but there is still much uncertainty as to what name is the proper one. The type specimen is lost so far as known.

Table 6 presented here is of specimens from KUMNH, all from Santa Caecilia, Napo, Ecuador.

Caecilia tenuissima sp. nov.

(Figs. 32-33)

Holotype: USNM No. 12353, from Guayaquil, Ecuador.

Diagnosis: A slender elongate species reaching a known length of 390 mm with a head width of 5.7 mm. Primary folds, 186, incomplete for the most part, with 9 secondary folds. Scales present at least in the last 10 to 15 cm of body; no subdermals found; eye in socket; narial plugs pointed; tongue darkened.

Description of the Holotype: Specimen defective with top part of the head opened and the brain removed, and parts of the palatal area and the jaws injured. Practically all of the significant features of the animal can be determined. The meas-

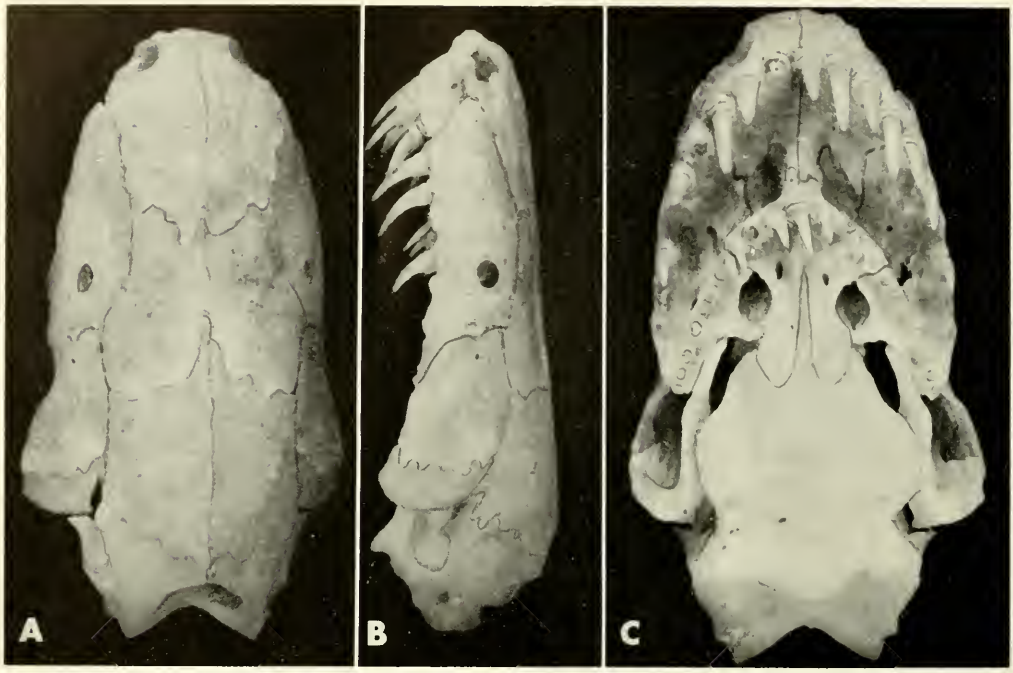

FIG. 31. *Caecilia tentaculata* Linnaeus. Skull, much enlarged.

urements of the head are, to a degree, estimated.

Head narrowing slightly anteriorly, the approximate width 5.7 mm; nuchal collars not clearly defined above, distinct ventrally, seemingly without transverse grooves dorsally; the distance from tip of snout to the third nuchal groove, 12.1 mm. The total length (stretched to eliminate kinks), 390 mm. The average height of the body approximately 4.8 mm. Eye, in a socket, seemingly invisible externally. The tentacular aperture below but definitely posterior to the nostril, its distance from the eye 2.8 mm, from the nostril 1 mm. The palate is injured but one small choana is visible. The tongue is somewhat pigmented, the narial plugs elevated and pointed. There are 186 primary folds (difficult to count), incomplete above and below throughout much of the body. There are 9 secondaries, 4 complete. A small unsegmented terminal shield, below which is the circular vent with 6 denticles posterior and 5 anterior to it. Anal glands not evident (probably a female). Scales are present in the last 10-15 cm of the body. Only a single scale row in the last folds, with a few other scattered smaller scales. The largest scales at a point 10 cm from terminus, 0.5 x 0.2 mm; in last cm the largest scales 1.3 x 1.1 mm.

Dentition: Premaxillary-maxillary teeth, 11-?; prevomeropalatine, 11-7; dentary, 9-?; splenial, 2-2. There seems to be no evidence of group-loss and group-replacement of the teeth.

Measurements in mm: Total length, 390; body height, 4.8, 4.5 posteriorly; height in length about 81 times. The body is slightly compressed, the width is about 3.5.

Color: Rather dark brown, vaguely lighter on lower part of head. Anterior part of body a little lighter than posterior. Top and sides of head whitish or yellowish in life, with blackish pigment about the tentacular area; some dark pigment on

the front of both jaws. A cream or whitish flecking extends irregularly over the whole body.

Remarks: This specimen was originally referred by Dunn (1942) to *Caecilia pachynema,* seemingly an incorrect association since it lacks all trace of the yellow broken stripe on the body. Its other characteristics also remove it from that form.

Oscaecilia bassleri (Dunn)

Data have been taken on the following specimens and here recorded: CAS No. 11654, Río Ampayacú, Pevas, Perú; KUMNH Nos. 125329, 125331, 127316, 127317, Lago Agrio, Napo, Ecuador, elev. 330 m.

Oscaecilia equatorialis sp. nov.
(Figs. 34-36)

Holotype: USNM No. 166421, from Dyott Farm, Km 121 from Quito, 6 km E Santo Domingo de los Colorados, Pichincha, Ecuador, collected by Dr. James Peters.

Diagnosis: A medium-sized species with slender elongate body, the length 432 mm, the body width 5 mm. Width in length 86 times. No eye-socket; the eye covered by bone. Primary folds 180, mostly incomplete dorsally; secondary folds 10, only 1 complete. Scales begin about 13 cm before terminus. A single row of scales in the terminal folds. Head grayish white;

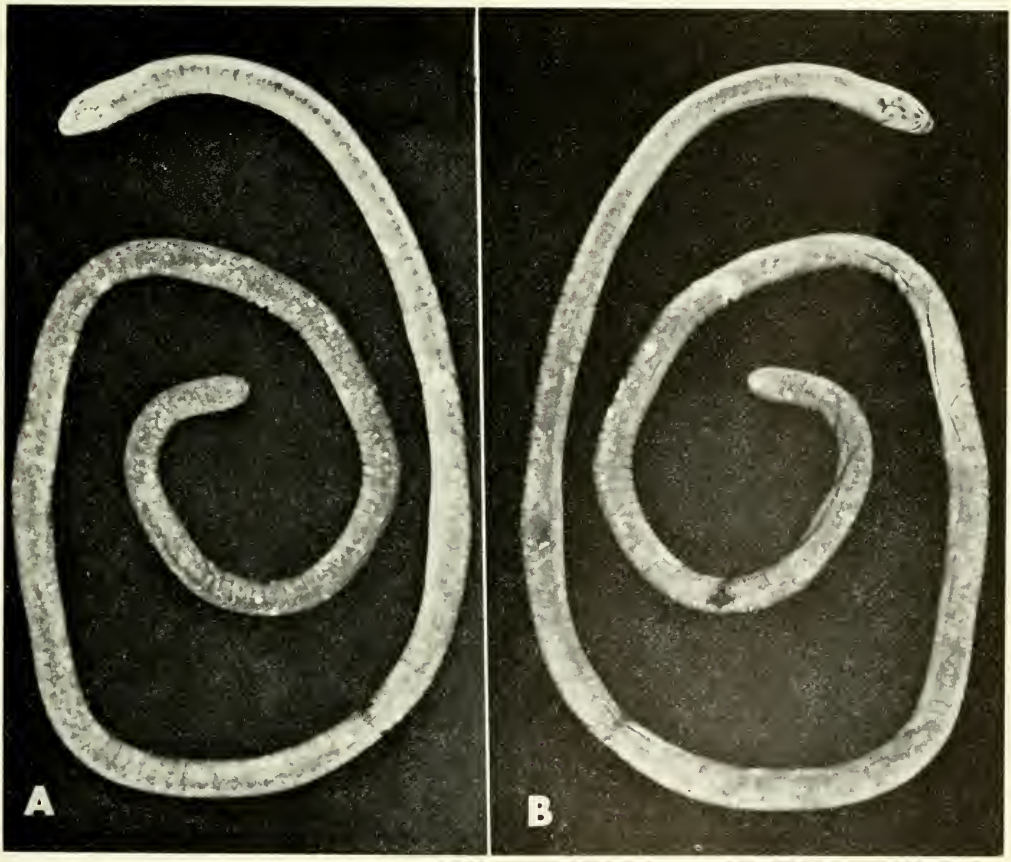

Fig. 32. *Caecilia tenuissima* sp. nov. Type. USNM No. 12353. Guayaquil, Ecuador. **A,** Dorsal view; **B,** ventral view. Length, 390 mm.

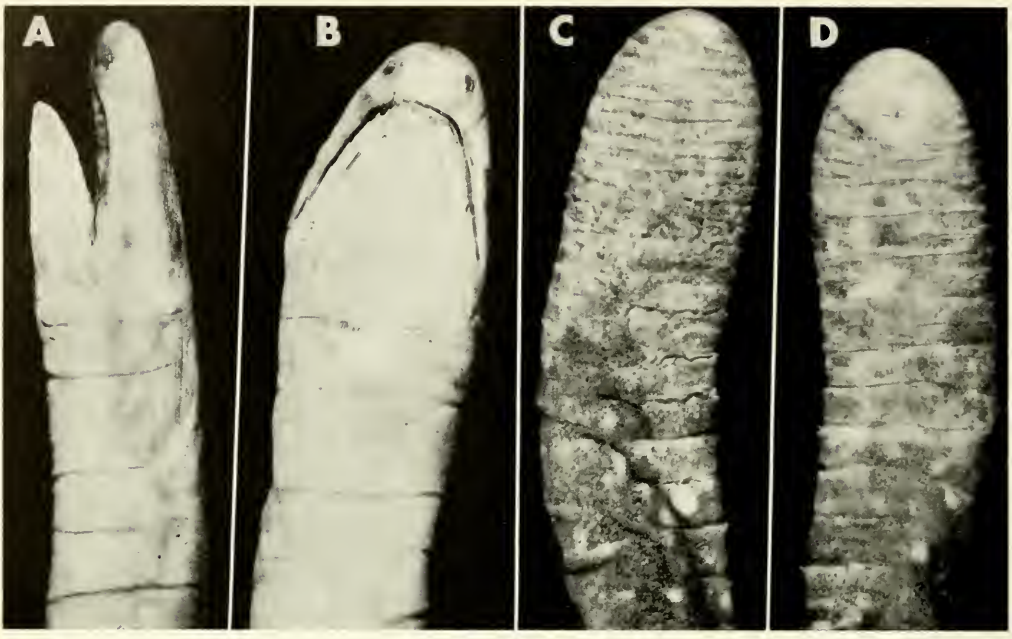

FIG. 33. *Caecilia tenuissima* sp. nov. Type. USNM No. 12353. Guayaquil, Ecuador. **A-B,** Lateral and ventral views of head; **C-D,** dorsal and ventral views of terminal part of body.

terminus, including the anal area, cream white.

DESCRIPTION OF THE HOLOTYPE: A very slender caecilian reaching a known length of 432 mm and with an average body width of 5 mm; the nuchal region for a distance of about 2.5 cm with a width of 6.6 mm. Eyes invisible externally, and if actually present covered with bone. The snout projects 1.5 mm beyond the mouth. First collar distinct, rather narrow, lacking a transverse groove; second collar separated from first by a groove laterally, but fused both above and below with the first primary fold and lacking a transverse groove. Nostrils plainly visible from directly above the head; the tentacular aperture almost directly below the nostril, its distance from the eye, 2.5 mm, from the nostril, 1 mm. Terminus of the body

TABLE 7. Data on *Oscaecilia bassleri* (measurements in mm).

Numbers	11654	125329	125331 ♂	127316	127317
Length	586	570	785	865	849
Head width	5	6.7	8.9	7.7	8
Body width	6.2	7	8	6.8	7
Body width in length	94	81	98	127	121
Tentacle to eye	3.1	3	3.5	4	4.1
Tentacle to nostril	0.9	1.1	1.1	1.1	1.2
Snout projects	1.4	1.7	2.2	2.3	2
Primary folds	249	236	250	254	260
mostly incomplete	yes	yes	yes	yes	yes
Secondaries	16	31	30	40	34
Sec. complete	4	7	5	6	2
Scales begin about last	1/5	1/4-1/5	1/5	1/5	1/5
Rows in posterior folds	1	1	1	1	1
Eye under bone	yes	yes	yes	yes	yes

Fig. 34. *Oscaecilia equatorialis* sp. nov. Type. USNM No. 166421. Pichincha Province, Ecuador. Length, 432 mm.

slightly swollen with a small unsegmented terminal "shield."

Primary folds 180 following the collars, the folds incomplete throughout most of the body save the last few cm. Secondary folds 10, with only one complete. Scales present at the beginning of the last third of the body. At first only 1 or 2 scales in a fold on each side, but just before the secondaries begin there may be a nearly complete scale row. Scales in the secondaries are about the same size as those in the primaries, and the final secondary row may also be complete. The largest scales seen measured 1 x 1.3 mm. Choanae moderate in size, the diameter of one equals the distance between them. The sex is seemingly female as no anal glands are evident. No subdermal scales have been found.

Dentition: If group-loss and group-replacement of teeth occurs it is not obvious at this time. The tooth formulae: premaxillary-maxillary, 9-1-10; prevomero-palatine, 8-1-9; dentary, 8-8; splenial, 3-3.

Color: The head is grayish above and below, and probably whitish or yellowish in life; neck lighter than the rest of the body, which is a blackish slate except for the terminus and subterminal area which are whitish.

Measurements in mm: Total length, 432; width of head, 5.8; width of body, 5; snout tip to first nuchal groove, 7.7; to second groove, 9.5; to third, 11.9.

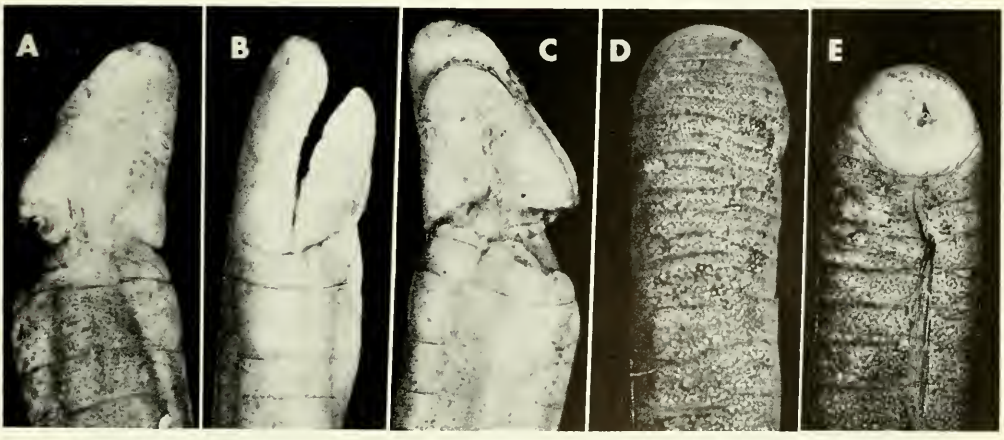

Fig. 35. *Oscaecilia equatorialis* sp. nov. Type. USNM No. 166421. Pichincha Province, Ecuador. **A,** Dorsal head region; **B,** lateral region of head and neck; **C,** ventral view of head and neck; **D,** posterior body, dorsal view; **E,** subterminal area, ventral view.

REMARKS: The specimen has been injured, the head being partially severed; otherwise it is in reasonably good condition. Figure 34 appears somewhat lighter than the specimen. The shape and character of the terminus are indicated in Figure 35.

Oscaecilia ochrocephala ochrocephala (Cope)

Two specimens, LACMNH Nos. 2719 and 2720, are from El Llano, one mile from Río Bayano, Panamá. These measure respectively 410 and 353 mm in length, and the folds respectively are primary, 180, secondary, 19, and 181, 16. In each there are 3 complete secondaries. The width in length is 60.3 and 50.4 times respectively. Thus both are within the known ranges of variation.

The following key will assist in contrasting the known species of the genus:

KEY TO SPECIES OF OSCAECILIA

1. "No scales" in folds (subdermals present), "no secondaries." Primaries, 226-231; "eye invisible"; length, 500-620 mm; width in length, 83-89 times. (Types destroyed) ..... *elongata* Dunn
—Scales present in folds; secondaries present 2
2. Primaries, 225-290 3
—Primaries, 140-210 4
3. Primaries, 249-286; secondaries, 17-54; vertebrae, 273±; total length to 975 mm; width in length, 80-107 times; a very small unsegmented terminal shield. Perú, Ecuador, Colombia ..... *bassleri* (Dunn)
—Primaries, 226; secondaries, 4; vertebrae (estimated), 231; length to 640 mm; width in length, about 91 times; a rather large unsegmented terminal "shield." Santa Caterina, Brasil ..... *hypereumeces* Taylor
4. Body with dark transverse rings 5
—Body lacking dark rings 6
5. Primaries, 169-189; secondaries, 7-29; length to 617 mm; width in length, 40-60 times; body ringed with black at edges of folds; head yellowish; scales begin about the 25th fold. Panamá and Northern Colombia .. *ochrocephala ochrocephala* Cope
—Primaries, 202-207; secondaries, 10-17; length to 686 mm; width in length, about 57 times; scales begin about the 24th fold;

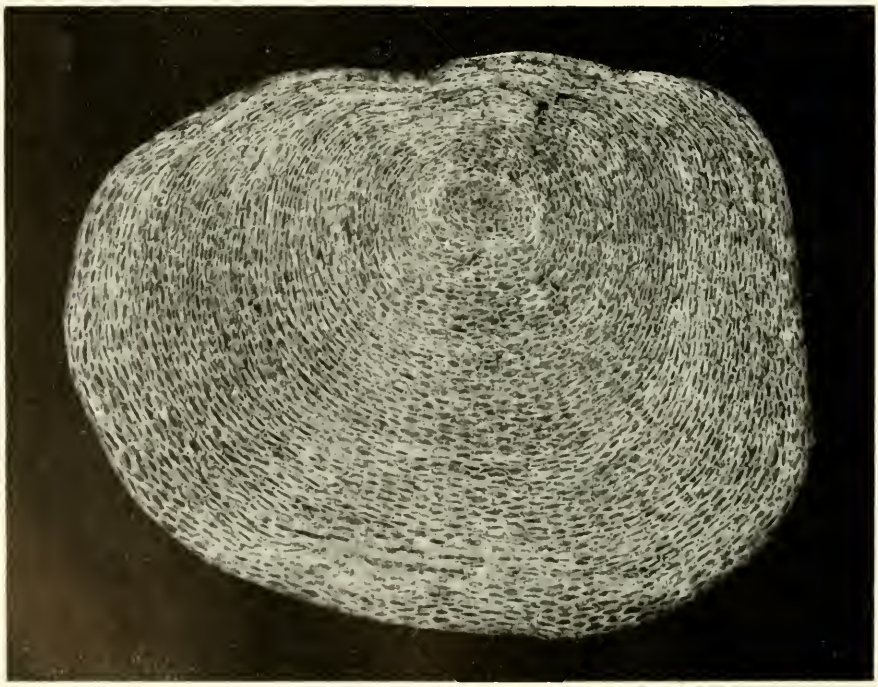

FIG. 36. *Oscaecilia equatorialis* sp. nov. Type. USNM No. 166421. Scale from last cm of body, 1 x 1.3 mm.

head slender; terminus wider than head. W. Colombia .... *ochrocephala polyzona* (Fisher)

6. Primaries, 146-147; secondaries, 16-17; length to 234 mm; width in length, 40-47 times; vertebrae, 151-153; grayish lavender above, ventrolateral region and venter whitish. Guyana .... *zweifeli* Taylor

—Primaries, 180; secondaries, 10; length to 430 mm; width in length, 86 times; body generally blackish or slate, head grayish white, terminus and subterminal area white. Pacific drainage, Ecuador .... *equatorialis* sp. nov.

Microcaecilia albiceps (Boulenger)

Dermophis albiceps Boulenger, Cat. Batr. Grad. s. Caud. and Batr. Apoda etc., 2nd ed., 1882, p. 98, figs. 1, 1a. Type-locality, Ecuador.

Besides data recorded on 11 specimens by me in my 1968 book, a further series of 15 specimens, all from Ecuador, has become available: 8 from Kansas University, 6 from the Los Angeles Co. Museum, and one from the California Academy.

The specimens from the Los Angeles Museum vary in length from 142 to 227 mm; in body width from 4 to 5.4 mm; the width in length from 34.6 to 45 times. The range of the primary folds is from 113 to 119.

More detailed data from the Kansas University and California Academy specimens are presented in Table 8. The longest specimen reaches a length of 240 mm. The primary folds vary between 112 and 123; the secondaries from 39 to 61, of which the complete secondaries number from 13 to 24.

Of the total of 26 specimens now studied all have been from Eastern Ecuador in the Atlantic drainage. I have no record of the species elsewhere in South America but it may be expected in countries bordering Ecuador.

Luetkenotyphlus brasiliensis (Lütken)

Siphonops brasiliensis Lütken, Vid. Medd. Nat. Foren Kjøbenhavn, 1851 (1852), p. 52. Type-locality, "Brasil".

Luetkenotyphlus brasilensis (Lütken), Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 588-592, figs. 320-322.

The type locality of this form was reported by me as "Brasil."

Table 8. Data on *Microcaecilia albiceps* (measurements in mm).

Number	10363	110612	106935	125324	125325	125326	125327	125328
Museum	CAS	KUMNH	KUMNH	KUMNH	KUMNH	KUMNH	KUMNH	KUMNH
Locality	Río Cotopino, Ecu.	Santa Caecilia, Ecu.	Limón Cocha, Ecu.	Lago Agrio, Ecu.	Lago Agrio, Ecu.	Lago Agrio, Ecu.	Lago Agrio, Ecu.	Lago Agrio, Ecu.
Total length	170	192	211	110	174	240	186	179
Width of head	4	4	4.1	3	4	4.7	4.1	4
Width of body	4.5	4.4	4	3	4	4.8	4.9	4.9
Width in length	38	43.5	44	36	43.5	50	38	36.5
Eye to tentacle	?	not vis.	0.6	0.3	0.5	not vis.	0.4	0.5
Tentacle to nostril	2.0	1.9	1.9	1.9	2.5	2.7	2.0	2.0
Snout length	1.0	1.0	1.0	.9	1.0	1.7	1.0	1.0
Snout tip to 1st groove	5.7	5.0	6.1	4.1	5.0	6.0	6	5.3
Snout tip to 2nd groove	7	6.8	7.5	5.4	6.8	8	7.5	6.8
Snout tip to 3rd groove	9.3	9	10.2	6.6	8.7	10.2	9.2	8.6
Primary folds	123	117	116	123	116	120	117	112
Secondary folds	61	47	44	55	39	52	53	43
Complete secondaries	19	15	13	?	14	24	18	18
Premax-max teeth	9-10	8-8	8-7	6-7	7-8	7-6	7-6	7-6
Prevom-pal teeth	13-12	15-14	15-15	11-12	12-13	13-14	13-12	13-14
Dentary teeth	10-10	10-11	11-11	10-10	11-11	11-11	11-11	12-12
Splenial teeth	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Scales begin about primary	15	?	?	20	18	12	15	21
Scales in middle body rows	3-4	3-4	3-4	3-4	3-4	3-4	3	3
Scales in terminal body rows	4	4-5	4	3-4	3-4	3-4	3	3

A letter from Dr. F. W. Braestrup of the Universitetets Zoologiske Museum, Kjøbenhavn, Danmark dated Dec. 11, 1971, makes the following statement: "In an old register there is an entry by Reinhardt dated Jan. 14, 1872 according to which the type of *Siphonops brasiliensis* Ltk. (merely said to be from Brasil) was collected at São Paulo 'sent by Dr. Langgaard'."

Herpele squalostoma (Stutchbury)

Two LACMNH specimens, Nos. 49715-16, from Vemba-Minzione Mayumbe, Lower Congo, have been available. Data, respectively, are as follows (measurements in mm): Length, 351, 216; head width, 7, 5.9; body width, 9.5, 7; eye under bone; snout tip to first nuchal groove, 8.7, 7; to second groove, 11, 8.1; to third, 15.1, 11; snout projects 2, 1.4. Nostril not visible from directly above head in either; tentacle in both, near lip; primary folds, 126, 125, in both all complete. Secondary folds, 43, 36; 5 complete in each. Scales in each begin about the 30th primary; 2-3 rows at middle, 4 rows posteriorly; largest scales measure about 2.0 x 1.8. Tooth formulae: premaxillary-maxillary, 14-13, prevomeropalatine, 14-15, dentary, 11-11 in both specimens; splenial, 2-2 in No. 49715. No terminal "shield"; width in length about 37, 31 times. The collars are complete, each with a transverse groove.

A third, living, specimen from the "Congo" was sent to me by Mr. C. D. Wellman. It was light grayish white but with rather a pinkish tinge on the anterior part of the body. It was maintained on earthworms, and later returned to the owner.

Schistometopum thomense (Barboza du Bocage)

LACMNH No. 35845, São Thomé, Gulf of Guinea, Africa. This specimen is 214 mm in length, the width (9 mm) in length approximately 24 times. Eyes visible in socket; the nostrils terminal, not visible from directly above head; tongue without narial plugs. Primary folds, 95; practically all complete. Secondary folds, 29; 7 complete. Tooth formulae: premaxillary-maxillary, 15-16; prevomeropalatine, 16-16; dentary, 12-12; splenial, 7-7. Scales begin at about the 21st primary; 4 scale rows in the terminal folds. The color is uniform yellow.

Siphonops annulatus (Mikan)

A very large number of specimens is available of this widely distributed South American species. I have recently examined a small series from Napo, Ecuador (LACMNH Nos. 73286-73290). The data are within the limits of variation published by Taylor (1968) based on more than 100 specimens.

On page 559 in Taylor, 1968, there appears an unaccountable error; it states that the variation in transverse primary folds is 112 to 130. On page 554 the variation is correctly stated as 78 to 98 folds.

It has been noted that the numbers 90-98 appear chiefly in Perú, Ecuador and Bolivia; those from the eastern range of the species usually vary between 80 and 90.

The greatest known length is 450 mm.

Siphonops hardyi Boulenger

Siphonops hardyi Boulenger, Ann. Mag. Nat. Hist., ser. 6, vol. 8, 1891, p. 457. Type-locality, Porto Real, Rio de Janeiro, Brasil.

A young specimen of this rare species is CAS No. 11653 from Rio Pedro Branca, Sierra Mantequeiras, Rio de Janeiro, Brasil, between Parati and Cunha (18 km from Parati). The number of primary folds is 93, within the known range of variation of 92-101. The total length is 129 mm. The eye is distinct in the socket.

Siphonops paulensis Boettger

The type-locality of *paulensis* is São

Paulo, Brasil. It has a wide distribution in South America. I have recently examined CAS No. 49897 from Rio Grande do Norte, Brasil.

Dermophis gracilior (Günther)*

Gymnopis gracilior Günther, Biol. Cent. Amer., 1892, p. 306, pl. 76, fig. 13. Type-locality, Chiriquí, Panamá.

The British Museum type and two specimens in the California Academy of Sciences were listed by Dunn (1942) under the name *Gymnopis mexicana gracilior*. He listed also a fourth specimen, BMNH No. 1907.6.28.27, from Pozo Azul, Costa Rica. This latter however is a different species. I have recently examined all of these specimens. It becomes apparent that none of these is related subspecifically with *Dermophis mexicanus* (Duméril and Bibron). Among the four specimens, Dunn gives as the variational range of the primaries, 95 to 102; of the secondaries, 32 to 78. My counts for the type and CAS specimens are 94 to 99 for primaries and 68 to 78 for secondaries.

Günther seemingly has erred in stating that the secondaries begin at the 40th fold since his figure shows them beginning at the 14th fold!

Taylor (1952) referred a Costa Rican specimen to the name *Dermophis mexicanus gracilior* but this specimen was later made the type of another species.

The CAS specimen No. 79463 from Boquete, Panamá, is a pregnant female of *gracilior* 323 mm in length. The uterine young are relatively light-colored, almost white on the venter. The transverse darker lines are not evident. Their heads are somewhat darker than the dorsum. At this stage the tentacular aperture is evident and in some the tentacles are protruding. The lower jaw has numerous rows of larval teeth. The primary folds are as yet poorly developed and cannot be counted. The six embryos measure 106, 107, 107, 107, 110, and 111 mm in length.

Dermophis mexicanus eburatus Taylor*

Due to the courtesy of Dr. Alan Leviton I have been able to examine a good series of these caecilians collected by Mr. Slevin at or near Volcań Isalco, Salvador. This series is numbered CAS 69627-69658 (two or three of the series wanting). Table 9 gives pertinent comparative data on these specimens.

Unfortunately the exact type-locality of *D. mexicanus* is presumably unknown, and larger series from the northern range may invalidate *eburatus*.

The Table shows a range of primaries between 104 and 112, the mean being about 107; the secondaries show a wider range, 61-88, the mean being about 75. The number of teeth increases with length of body (age). Scales in the folds begin between the 8th and 14th primaries. Where they first appear anteriorly there may be only a single scale in each side of the fold, but there are 6-7 scale rows in the posterior folds. The largest scales may measure 3 mm in greatest dimension.

The position of the tentacular aperture is below eye level, more than twice as far from the nostril as from the eye, as is typical of the genus *Dermophis*. Body width in length varies between 15 and 24 times.

With an examination of this material I am of the opinion that *Dermophis eburatus* is probably not worthy of specific distinction.

Since the exact type-locality of *mexicanus* is not known ("Mexico"), it will be uncertain whether any Mexican population is subspecifically distinct from *eburatus*. It is probable that the scale rows of *m. ebu-*

* Since this paper went to press a paper on the partial revision of the genera *Dermophis* and *Gymnopis* has appeared by Savage and Wake (Copeia, 1972, no. 4, p. 680). This is Savage's second attempt at a revision of these genera, the first appearing in Trans. Kansas Acad. Sci., vol. 56, no. 3, 1953, pp. 321-324. One should look forward to his next several revisions.

TABLE 9. Data on *Dermophis mexicanus eburatus* (measurements in mm).

Number (CAS)	Body length	Body width	Head width	Body width in length about	Primary folds	Secondary folds	Complete secondary folds	Premaxmax teeth	Prevompalat. teeth	Dentary teeth	Splenial teeth
69627	135	7	6	19	105	77	12				
69628	165	8	7	20.6	110	83	—				
69629	174	10	7	17.4	104	75	—				
69630	170	8.4	7	20	106	68	—				
69631	267	13	10	20.5	112	74	—				
69632	165	7.5	6.2	22	108	88	—				
69634	145	8	7	21	109	74	12				
60636	140	7	6	20	106	79	8				
69637	173	7.2	6.2	24	108	70	—				
69638	123	6	6	20	107	69	7				
69639	179	9	6.8	19	106	72	—				
69640	246	10.1	9	24.3	106	76	—				
69641	311	18	17	17	107	67	6	17-16	16-17	15-16	0-0
69642	321	18	11.8	18	107	79	10	19-19	22-21	15-15	0-0
69643	244	13	8.4	19	109	71	—	——	——	——	—
696'4	192	9.9	7.7	19.5	108	71	—	——	——	——	—
69645	280	14	11.4	20	107	61	8	17-15	15-16	13-13	0-0
69646	210	9.8	8	21	108	84	—	——	——	——	—
69647	—	—	—	—	109	75	12	19-18	19-18	14-15	0-0
69618	285	13.3	13	21.5	104	69	—	——	——	——	—
69649	331	17	12	19.4	106	76	10	19-18	17-18	15-15	0-0
69650	231	10	8	23	108	73	—	——	——	——	—
69652	354	19.8	13.5	17.8	106	68	10	19-20	20-20	18-18	0-0
69654	395	19	14	21	106	64	8	21-20	21-22	16-16	0-0
69655	357	23	14	15.5	105	—	—	17-18	17-18	15-15	0-0
69658	406	21	14	19	107	88	8	19-18	22-21	15-15	0-0

ratus exceed those in *mexicanus* since certain specimens of *mexicanus* examined show only 3 or 4 scale rows posteriorly in each fold. The number is larger, 6-7, in *m. eburatus*.

Geotrypetes grandisonae Taylor

(Figs. 37-38)

Geotrypetes grandisonae Taylor, Univ. Kansas Sci. Bull., vol. 48, no. 23, 1970, pp. 849-855, figs. 1-4.

A recent paper of Largen, Morris and

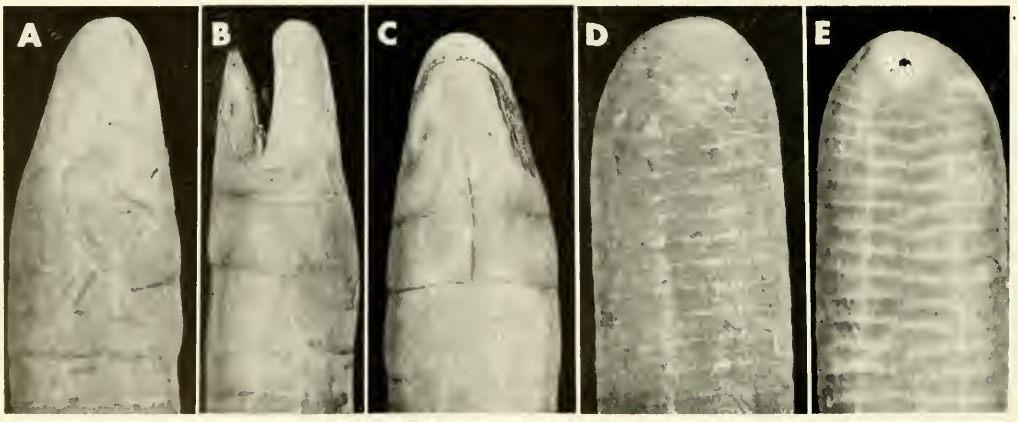

FIG. 37. *Geotrypetes grandisonae* Taylor. BMNH specimen from a point east of Buna village near Jimma Kaffa, Ethiopia. **A-C,** Dorsal, lateral and ventral views of head; **D-E,** dorsal and ventral views of the terminus of the body.

Yalden (1972) gives a splendid report on a series of 30 specimens, nearly all larvae. Dr. Largen has had the kindness to send the specimens for me to examine.

Among the larvae is one specimen (No. 23 from Abiu, near Gore, Ethiopia) approximately 57 mm in length. While it is difficult in most species to classify the larvae, I strongly suspect that this tiny specimen represents a species different from

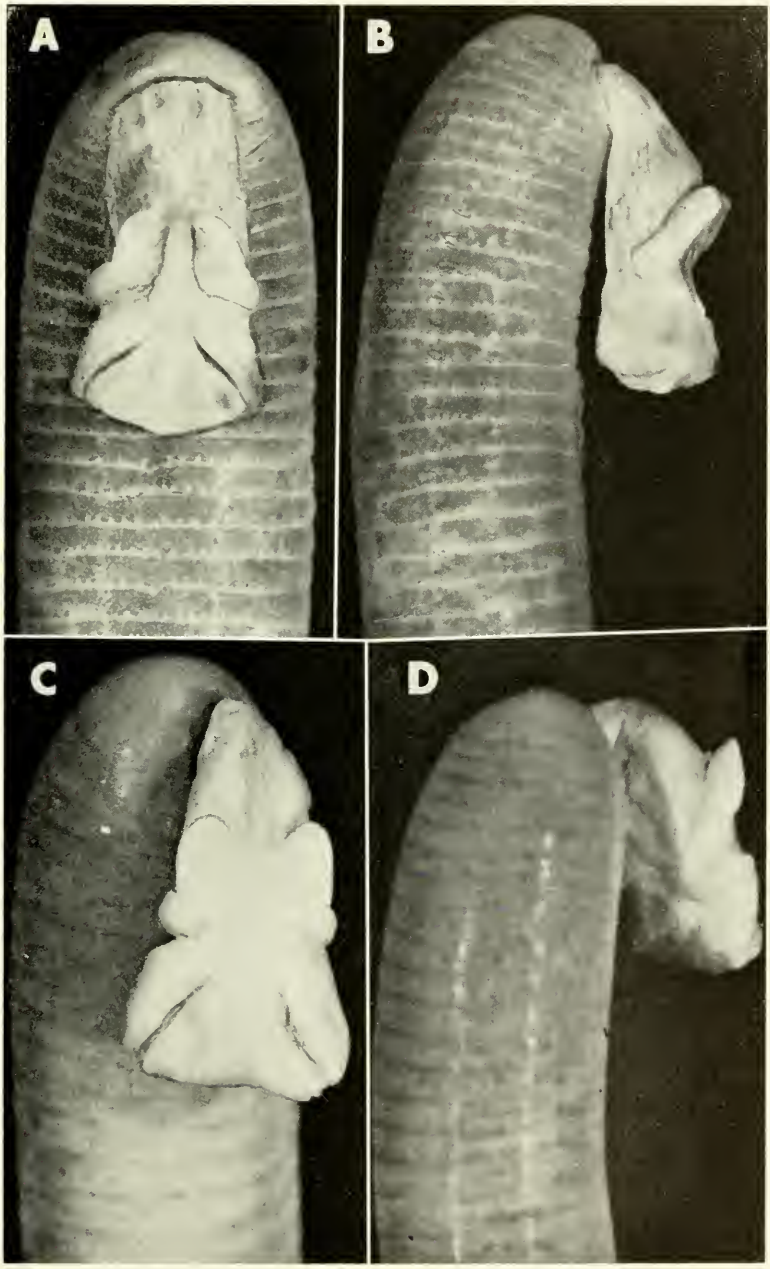

Fig. 38. *Geotrypetes grandisonae* Taylor. **A-B,** Ventral and lateral views of extruded penis; **C-D,** ventral and lateral views of second specimen with extruded penis.

the other larvae, and actually may be the young of one of the diminutive genera, *Afrocaecilia* or *Boulengerula,* that occur in the neighboring country of Kenya. This opinion is based on the very diminutive size of the specimen and the fact that there is greater loss of larval characteristics of the labial region of the mouth. This suggests that it is more mature than all the other larval specimens that are considerably larger.

I include figures of the anterior and posterior parts of the body (Fig. 37) and of the penial structures of two adult specimens (Fig. 38) despite the fact that a good figure of these structures is given in the paper mentioned.

Geotrypetes seraphini congoensis Taylor

Geotrypetes congoensis Taylor, Caecilians of the World, Univ. Kansas Press, 1968, pp. 715-718, figs. 392, 393. Type-locality, Kitadi, "riv. Sinda," Mayumbe Region, Congo. (Kiva as a locality is in error.)

Geotrypetes seraphini seraphini Laurent, Rev. Zool. Bot. Afr., vol. 63, 1961, pp. 262-266.

Taylor, in reporting the type-locality for this species, misinterpreted a handwritten invoice as to the locality. Kiva is actually on the eastern side of Congo; Mayumbe is western. Dr. Laurent calls attention to this error in a recent paper.

I have recently examined two specimens, CAS Nos. 49714 and 118591, from Minkala River, Mayumbe, Congo.

I now regard *congoensis* as a subspecies of *G. seraphini.*

Uraeotyphlus menoni Annandale

Uraeotyphlus menoni Annandale, Rec. Ind. Mus., vol. 9, pt. 5, no. 20, Dec. 1913, pp. 301-302. Type-locality, Trichur, Cochin, India.

Annandale states that the type of *menoni* has about 170 rings or folds plus 10 complete rings on the tail—thus a total of approximately 180. There was one co-type.

Seshachar (1939) also counted the primaries and secondaries on the same specimens and reported 197 for the type, ZSIC No. 16709, and 195 for the co-type, ZSIC No. 16695.

I have recently examined two specimens from Kottyam, India, Nos. 1216A, 1216B, private collection of Harlan D. Walley, Northern Illinois Univ., Dekalb, Ill., one of which has a total series of folds on body and tail of 179 and the other a total of 187. These are almost identical in color and markings.

Scolecomorphus vittatus Boulenger

Specimens LACMNH Nos. 35479-35482, and 35668 (young) have recently been studied and data taken. These vary in length from 140 mm to 324 mm.

All are from "Bunduki," Uluguru Mts., 5,000 ft. elev., Tanzania. The primary folds are 129-153, a few terminal ones complete; no secondaries; eye under bone (sometimes pulled forward to lie close to nostril); tongue without narial plugs; prevomeral and palatine dental series widely separated; tentacular termination large, bulbous; dentary teeth, 11-11; no splenial teeth; group-loss and group-replacement of teeth; no scales.

The range of primaries does not exceed that in many species of the order; the total known is 122-148 in this species (120-154 in the genus).

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TAXONOMIC AND ONTOGENETIC STUDIES OF COCKROACHES (BLATTARIA)

By

IVAN HUBER

Vol. 50, No. 6, pp. 233-332 June 28, 1974

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Taxonomic and Ontogenetic Studies of Cockroaches (Blattaria)

Ivan Huber

Taxonomic and Ontogenetic Studies of Cockroaches (Blattaria)[1, 2]

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ABSTRACT

A phenetic numerical taxonomic study of 37 species of cockroaches used 446 characters of the exoskeleton. Most species were represented by six stages which were the adults and first and last instar nymphs of both sexes. These were the Operational Taxonomic Units (OTU's) of the study. OTU's made up of combinations of the six stages were also used. *Q*-type analyses of correlations and taxonomic distances between pairs of OTU's were performed and the results were expressed as phenograms. The OTU's were represented in three-dimensional phenetic space (models) by means of centroid component analysis of the character correlations (*R*-type).

Comparisons of the similarity matrices of the six stages reveal closest correlation between the adult and last instar nymphs. Similarity matrices of small nymph males and females are most highly correlated; those of adults have the lowest correlations with each other. Phenograms and models of both sexes at each ontogenetic stage are compared. The phenetic and phyletic implications of the arrangements of OTU's are considered in detail. Changes with increasing age are studied in the models. The migrations of family clusters with changes in ontogenetic age are described and discussed. The seven data tables of McKittrick's study of cockroaches are also analyzed by the above procedures. The classifications derived from the latter and from my own data agree well with each other and with McKittrick's taxonomic arrangement. Since the classification of the nymphal stages uses different characters from those of McKittrick, this congruence is regarded as independent confirmation of her conclusions. The present study shows that the "convergence" between the adults of *Cryptocercus punctulatus* and *Panesthia australis* is the result of similar morphological specialization. The relationships of *Attaphila fungicola* are investigated and McKittrick's removal of this species from the Polyphagoidea to the Blattellidae is justified. The Polyphaginae is shown to be phenetically closest to the Blattoidea.

The models of cockroach OTU's at different instars accord well with von Baer's generalizations regarding differentiation of OTU's during ontogeny. A phenetic analogy to De Beer's morphological modes of evolution is demonstrated in my ontogenetic data. The effects of using large numbers of randomly selected characters are discussed and the factor asymptote is shown to have been exceeded. Nymphal characters, previously not exploited in blattarian taxonomy, are shown to be useful. Incongruence of classifications and mosaic evolution are examined in McKittrick's data and these phenomena are considered to be reasons for the partial rejection of the nonspecificity hypothesis. The usefulness of the model as a classification is discussed. Possible methods of producing a general classification are explored and it is noted that such a classification would be a compromise and result in loss of taxonomic information. General classifications based on a comparison of genomes are considered. It is

[1] Contribution No. 1494 from the Department of Entomology of the University of Kansas, Lawrence, Kansas. This study represents a portion of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree.
[2] This research was supported by grant GM-11935 from the National Institutes of Health to Dr. Robert R. Sokal.
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suggested that the wingless condition of some Blattaria is neotenic and that the suppressed characters, if still present in the genome, could be revealed by experimental treatment. Such individuals could then be subjected to morphometric analysis. Other suggesions for further application of these data are made.

1. INTRODUCTION

There is continuing controversy over the role of numerical taxonomy in systematics, therefore a means of assessing the usefulness of a numerically derived classification would be of value. In an attempt to accomplish this, numerically produced phenetic classifications of cockroaches are compared with an accepted, orthodox, phyletic classification, that of McKittrick (1964).

Both nymphal and adult cockroaches are used, for it is generally agreed that characters from all stages in the life history should be employed in constructing a classification. Uvarov (1966), in his book on locusts and grasshoppers, points out the potential importance of the study of nymphal characters in taxonomic analysis. Sokal and Sneath (1963), Rohlf (1963) and Kaesler (1967) call for increased emphasis on multivariate treatment of immature as well as adult forms. As yet, the only numerical taxonomic studies of this kind are those by Rohlf (1963, 1967) using mosquitoes, and Wrenn (1972) using trombiculid mites.

There are many instances where a classification using larval stages conflicts with one using the adult. These situations are reviewed by Emden (1957) and by Sokal and Sneath (1963). Many of these incongruences may be the result of ontogenetic change during evolution and the role of such changes is discussed by Orton (1953, 1955) and by De Beer (1958). The advantages of quantifying similarity in comparative ontogenetic studies is pointed out by Raven and Mertens (1965). The second purpose of this work is to obtain such quantitative information and to use this to initiate the study of ontogenetic divergence and convergence in the Blattaria.

Of the insects considered, the cockroaches seemed for many reasons, most suitable for an investigation of this kind. They form a homogeneous taxon, which perhaps explains the number of very different classifications that have been proposed for this group in the past. Previous numerical taxonomic studies of adult and immature insects have used only forms with a complete metamorphosis, where few, if any, characters are ontogenetically homologous. The cockroach however, has a gradual metamorphosis and a general similarity of form between the sexes which allow comparisons based on characters common to all stages. Finally, many species of cockroaches are available and easily cultured so that it is relatively simple to obtain the immature stages.

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2. MATERIALS AND METHODS

2.1. Specimens: The thirty-seven species of cockroaches used were intended to represent the morphological diversity encountered within the Blattaria (Table 1). Both sexes of adults, last instar nymphs (referred to as large nymphs) and first instar nymphs (small nymphs) were obtained for most species. Each of the six was an Operational Taxonomic Unit, or OTU (Tables 1, 2).

Most small nymph OTU's consisted of nymphs collected within 24 hours of hatching. These were assumed to be in the first instar. Other small nymphs were the youngest obtainable, probably representing no more than the second instar (Table 1). The specimens selected for the large nymph OTU's were the biggest from large cultures having a wide range of nymphal sizes and were presumably in the last nymphal instar. In some cases, the instar was confirmed where adult wings or external genitalia were detected within the nymphal organs. Ross and Cochran's (1960) and Lawson and Lawson's (1965) criteria were used to sex the first instar nymphs. The first instar female of *Cryptocercus punctulatus, Lophoblatta fissa, Supella longipalpa* and *Platyzosteria melanaria* was difficult to identify because the deep median slit usually present on the ninth sternum and absent in the male is reduced to a slight emargination in these species.

In most cases, three specimens were employed for each OTU, though this was not always possible (Tables 1, 2). Ten specimens per OTU of *Periplaneta americana* and *Leucophaea maderae* were used for special statistical tests. There was no marked variation among the specimens of a single OTU, with the exception of adult males of *Byrsotria fumigata* where there are both macropterous and brachypterous forms. This OTU, therefore, included one of each form and an apparently

intermediate specimen. Of the three large nymph males of *B. fumigata,* one was selected because of its noticeably longer wing pads, indicating probable development into a macropterous adult. Thus, the means of character values represented phenetically intermediate points between the morphological types.

Material was preserved as follows. Specimens were killed by brief immersion in boiling water. Those less than 2.5 cm in length were placed intact into Dietrich's Fixative.[4] In larger specimens, the pleural membranes of two or three abdominal segments were slit on the left side to facilitate penetration of the fixative. After 24 hours the specimens were given two 24-hour washes of 50% ethyl alcohol, then stored in 70% ethyl alcohol containing a few drops of glycerine to prevent drying out. Some pinned specimens had to be included in the study for more complete representation and these were also stored in 70% alcohol. The color patterns of pinned material did not apparently differ from the fixed and preserved specimens.

In a preliminary study, 29 head measurements from five pinned and ten fixed adult female *Periplaneta americana* were compared by an analysis of variance. Since only six of the 29 measurements showed statistically significant differences between pinned and fixed specimens, and since only a small percentage of the total number of characters were measurements (Table 3), the value of using the additional pinned specimens (Table 1) seemed to outweigh any introduced bias.

2.2. Characters: Four hundred and forty-six characters, drawn from the external exoskeleton of all body regions, were recorded for each specimen. The only selective criterion for a character was that it showed variation in the 177 "real" OTU's. Some characters were quantitative, others concerned color, pattern, absence, presence, shape, or relationship of structures (Table 3). To facilitate treatment of the data, characters were classified into two types, 1) independent, and 2) dependent on the state of another character. An example of a type 2 character is "number of branches of the Cu vein of the forewing." This could be recorded only if Cu was distinguishable from vein M. Male genital characters were NC (no comparison) in female specimens, while most, though not all, female genital characters were NC in male specimens. The genital characters were usually NC in the nymphs, because the organs were rudimentary. An annotated list of characters is available.

Measurements were made with a Bausch & Lomb filar micrometer. Structures too large for the microscope field were measured with a millimeter ruler under a magnifying glass. All measurements were converted to microns by the computer program which averaged the values for all specimens of one OTU.

2.3. Treatment of data: The data were processed by IBM 7040 and GE 625 computers at the Computation Center of the University of Kansas, using the NT-SYS system of programs developed for numerical taxonomy by F. J. Rohlf, R. Bartcher and J. Kishpaugh. For information concerning the computational techniques described here, see Sokal and Sneath (1963).

The six original OTU's were individually analyzed. Two new kinds of OTU's were also constructed as follows: 1) the sum (723) of the combined adult characters, and 2) the sum (1547) of the combined characters of all six stages. The discrepancy between the numbers above and the numbers of available characters is due to invariance. In order to represent material not available in the present study

[4] The formula used is: Distilled Water, 300cc; Formaldehyde, 50cc; Ethyl Alcohol—95%, 150cc; Glacial Acetic Acid, 10 cc. This differs in proportions from the formula given by Gray (1954).

(Table 2), 54 "dummy" OTU's consisting of NC's, supplemented the "real" OTU's. OTU's were also formed for both male and female genital characters.

Similarity matrices were calculated using a single variate for each character in each OTU. Variates of type 1 characters were averaged, ignoring NC's. But the presence of NC values in type 2 characters made a special conservative procedure necessary for the averaging of variates. If NC's predominated, that character was regarded as NC for the OTU. Where there were ties in the two- and ten-specimen sets a character was considered as NC.

All characters were standardized. Pearson product-moment correlation coefficients *(r)* and coefficients of taxonomic distance *(d)* between pairs of OTU's were calculated. Values for *r* between pairs of characters were also obtained.

The unweighted pair-group method of cluster analysis using arithmetic averages (UPGMA) was performed on the Q-study correlation and distance matrices. Results were expressed as phenograms (Mayr, 1965; Camin and Sokal, 1965). How well a phenogram agreed with its similarity matrix was expressed as the cophenetic correlation coefficient (r_{coph}) (see legends of phenograms). Only cophenetic correlations greater than 0.5 were presumed significantly different from zero (Rohlf, pers. comm.).

One of the options of NT-SYS is the SORTIT routine, which ranks the similarity coefficients of each column of a similarity matrix. In discussions of the rankings of OTU's in a column, the nominate OTU was the one against which all others in the column were ranked and was thus designated as "first." Two OTU's were said to "pair" when they ranked mutually closest in each other's columns. These rankings proved extremely useful in analysis of unexpected groups in the phenograms where two clustering OTU's were not necessarily also paired.

Phenetic relationships of the OTU's were also illustrated by 3-dimensional models (Rohlf, 1967, 1968; Moss, 1967; Hendrickson and Sokal, 1968). Characters with more than one NC were eliminated from the matrix of standardized values because of the distortion they produced. Correlation coefficients between characters were then calculated. Zeros were inserted in the matrix of correlation coefficients where remaining NC's prevented the calculation of values. Three factors were extracted from this matrix by centroid component analysis, which is more economical of computer time than principal component analysis. Finally, the calculation, matrix of factor loadings $\times$ matrix of standardized characters, produced a matrix of projections (or coordinates) in the three factor dimensions for each OTU. The models were constructed from these projection matrices.

Distances *(d)* between the OTU's in the models were computed by treating each of the three factors of the projection matrix as a composite character. After standardizing the new character values, distances between OTU's (centroid distances) were calculated. The matrices of these distances were processed by the SORTIT program and also clustered, so that cophenetic correlations could be computed between them and their phenograms (see legends of photographs).

McKittrick's (1964) data matrices were treated by the techniques described above. Only the species of the present study were included except for a few cases where it was necessary to use closely related forms. The number of characters in her data matrices was reduced ("condensed characters"); e.g., in her Table 1, char. 39 and 40, "no median sclerite" and "median sclerite present," were combined into a single character, "median sclerite present

or absent." All McKittrick's characters, which were relatively few in number, were used for the centroid component analysis.

Except where otherwise indicated, all citations of McKittrick's work refer to her 1964 monograph.

A comparison was desirable between McKittrick's own interpretation of her results, i.e. her phylograms, and the phenograms computed from her data by me. For this, interpretive phenograms were prepared from the phylograms, presenting the phyletic relationships as phenetic ones. Arbitrary, successive, numbers were assigned to each level of branching of the interpretive phenograms. These values were converted into a matrix of similarity coefficients using a program developed by Mr. John Kishpaugh. This matrix was then compared with the similarity matrix computed from McKittrick's data, by calculating the cophenetic correlation coefficient.

2.4. Data and annotated list of characters: An annotated list of characters, and the data and similarity matrices upon which this study is based, are available from the author. Magnetic tape copies may be obtained on request.

3. THE BLATTARIA OF THIS STUDY AND THEIR CLASSIFICATION ACCORDING TO McKITTRICK

The position of the Blattaria within the orthopteroid insects has frequently been changed. McKittrick discusses this and treats the cockroaches, termites and mantids as three suborders of the Dictyoptera. The classification of the cockroaches themselves has also been unstable. Princis (1960) reviews cockroach taxonomy and presents his own classification.

The classifications of Rehn (1951) and McKittrick are potentially useful for purposes of comparison in this study. These authors do not agree; McKittrick, for instance, separates the Blattidae from Blattellidae and Blaberidae while Rehn places them in a single taxon. Both authors make an analysis of organ systems. Rehn's conclusions are apparently based on wing structure alone. But Gurney (1951) states that observations on other structures, not mentioned by Rehn (1951), influenced the classification. Because of this and since he does not tabulate his data, Rehn's study was not used. In the case of McKittrick, tables summarize her observations and her classification is constructed from analysis of four different character systems (male and female genitalia, proventricular apparatus, and oviposition behavior). This makes her work ideal for comparison between the orthodox and statistical methods of analysis.

McKittrick's arrangement of the cockroaches is summarized in Table 4 and Figures 1, 5, 11, 19 and 20. Certain species used in the present work are of particular interest. In the Blattoidea, the family Cryptocercidae contains the single genus *Cryptocercus*. This is regarded as the most primitive surviving cockroach, exhibiting interesting morphological similarities to *Mastotermes darwiniensis*, the most primitive living termite. The latter, like the cockroaches, encloses its eggs in an ootheca, a trait lost by more advanced termites. On the other hand, *Cryptocercus* is xylophagous, possessing wood-digesting intestinal flagellates not found in other cockroaches. McKittrick (1964, 1965) discusses the relationships between the Isoptera and the Blattaria. The Blattidae are divided into three subfamilies, the Lamproblattinae (most closely related to the Cryptocercidae), the Blattinae (including the familiar pests *Periplaneta americana*, *Periplaneta australasiae* and *Blatta orientalis*) and the Polyzosteriinae. *Eurycotis floridana* is an interesting polyzosteriine which exudes a fruity-smelling defensive

secretion when roughly handled. Roth et al. (1956) identified the major active ingredient as 2-hexenal. This compound was found in certain Polyzosteriinae but in none of the Blattinae studied by Dateo and Roth (1967). They suggest its possible use as a taxonomic character. McKittrick and Mackerras (1965) propose a fourth subfamily, Tryonicinae, intermediate between the Lamproblattinae and the Blattinae, but it is not represented here.

Roth (1967b) regards the manner in which the ootheca is manipulated by the female as taxonomically significant and important in the development of internal incubation in the Blattaria. The ootheca is extruded with the keel in a dorsal position. All the Blattoidea and some of the Blaberoidea carry the ootheca in this position until it is deposited. Other species rotate the ootheca 90 degrees before dropping it or retracting it into the uterus.

McKittrick considers the Polyphagidae as the most primitive of the blaberoid families. One of the two subfamilies of the Polyphagidae, the Holocompsinae was unobtainable. However, *Polyphaga* and *Arenivaga* of the Polyphaginae were included in this study. These deserticolous genera are sexually dimorphic, the female is round and apterous while the male is elongate and macropterous. Some of the polyphagids carry the egg case as do the blattoids, while others show "primitive rotation" where the anterior eggs are not within the vestibulum (Roth, 1967b).

The Blattellidae are divided into five subfamilies by McKittrick. The Anaplectinae (supposedly the most primitive), Nyctiborinae and Ectobiinae were not available for the present study. Among the Plectopterinae is the familiar brown-banded cockroach, *Supella longipalpa*. Apparently neither the Anaplectinae nor the Plectopterinae rotate the ootheca, though in the latter, the anterior eggs of the ootheca are inside the vestibulum (Roth, 1967b). The Blattellinae include the German cockroach *Blattella germanica* and the two native American species *Parcoblatta pensylvanica* and *Ischnoptera deropeltiformis*. The latter is not studied by McKittrick, but Roth (1967b, d) and the present author assign it to this subfamily. *Attaphila fungicola,* an inquiline of the Texas leaf-cutting ant *Atta texana,* is regarded by McKittrick (cited by Roth, 1968b) as a blattellid although Princis (1960) places it in his group Polyphagoidea. Roth (1968b) observes that the ovarioles of *Attaphila fungicola* resemble those of blattellids rather than those of polyphagids. I would agree that it belongs in the Blattellidae but, like Roth and McKittrick, would not assign it to any particular subfamily. The Blattellinae, Ectobiinae and Nyctiborinae exhibit "advanced rotation" where the anterior eggs in the ootheca are in close contact with the tissues of the vestibulum (Roth, 1967b). In most of the blattellids investigated by Roth and Willis (1955b), the ootheca is dropped shortly after formation, whether rotated or not, but in *Blattella* it is carried for the entire period of embryogenesis and the eggs absorb water from the female. Development of advanced rotation of the ootheca and absorption of water in the Blattellidae were probably important preadaptations for ovoviviparity (Roth, 1967b, c). Roth reviews ovariole structure (1968b) and rotation, structure and water content of the ootheca (1967b, c, 1968a) in the Blattaria and correlates differences with the evolution of ovoviviparity.

The Blaberidae are distinguished by the presence of a brood sac, or uterus, in the female. The ootheca is formed as in other cockroaches, then rotated and retracted into the brood sac where the eggs absorb water (Roth, 1967c). *Diploptera punctata* is actually viviparous, since there is also an increase in dry matter during

embryogenesis (Roth and Willis, 1955a).

According to McKittrick, the Blaberidae fall into three groups or "complexes" (Table 4). The three subfamilies of the first or blaberoin complex are the Zetoborinae, the Blaberinae and the Panesthiinae. The best known of the Blaberinae represented in this study is *Blaberus,* a genus of large tropical cockroaches. *Panesthia australis* of the Panesthiinae is noteworthy because of its striking superficial resemblance to *Cryptocercus punctulatus.* Both species are xylophagous, but where *C. punctulatus* possesses symbiotic intestinal flagellates, *P. australis* harbors bacteria, amoebae and ciliates (see McKittrick, 1965, for references). The two species also show important differences in the character systems investigated by McKittrick.

The panchloroin complex with its four subfamilies (Table 4) is well represented in this study. The Pycnoscelinae includes *Pycnoscelus surinamensis* and *Pycnoscelus indicus,* sibling species of the Surinam cockroach, one of which is parthenogenetic. Roth (1967a) applies *P. surinamensis* to the parthenogenetic and *P. indicus* to the bisexual form. The Diplopterinae is represented by the viviparous *Diploptera punctata* and the Panchlorinae by the Cuban cockroach, *Panchlora nivea,* which is green as an adult. The Madeira cockroach, *Leucophaea maderae,* and *Gromphadorhina portentosa,* a large apterous species which produces hissing sounds, belong to the Oxyhaloinae. The representatives of the epilamproin complex both belong to the Epilamprinae, since none of the Perisphaeriinae was available.

4. ANALYSIS AND DISCUSSION OF McKITTRICK'S DATA

4.1. McKittrick's Table 1: The oviposition behavior, structure of the proventriculus, male and female genitalia in the subfamilies of the Blattaria

In Table 1 McKittrick provides data on the above character systems for all the subfamilies of the Blattaria and constructs a phylogram (Fig. 1) from this information. The 15 subfamilies represented in my study (Table 5) were selected as OTU's. Forty-six of McKittrick's 66 characters were retained for analysis, condensation or invariance (because of the reduced number of OTU's) eliminating the others. Correlation (Fig. 2) and distance phenograms and a model (Fig. 3) were prepared. (The branching sequences of the correlation and distance phenograms are identical and therefore the latter is not considered further.)

Interpretive phenograms are used in an attempt to resolve the trifurcations of the phylogram into the bifurcations required by the computed phenograms. There are several such trifurcations in Figure 1, e.g. at the base of the Blaberidae where it is not clear whether the epilamproin complex clusters with the blaberoins or the panchloroins. A number of interpretive phenograms of Figure 1 are possible:

1. The arrangement illustrated in Figure 4.

2. The Panesthiinae and Blaberinae unite before joining the Zetoborinae.

3. The Polyphagidae and Blattellidae unite before joining the Blaberidae.

4. Arrangements 2 and 3 are both present.

1A, 2A, 3A, 4A. These resemble 1, 2, 3, and 4 respectively but the epilamproin complex joins the panchloroin complex.

Cophenetic correlation coefficients between each of the above and the original matrix of correlations based on McKittrick's Table 1 are good (0.820 to 0.828). The small range of these values suggests that the phenograms are all equally valid interpretations of the phylogram (supporting McKittrick's use of trifurcations). Should the selection of one arrangement be necessary where, as in this case, there

is no statistical basis for a choice, the numerical taxonomist must use other, perhaps subjective, criteria. Sokal and Sneath (1963), Sokal and Michener (1967) and Moss (1967) discuss similar problems with phenograms produced by different methods of cluster analysis.

Of the eight phenograms discussed above, the author prefers 1A or 2A. This decision is based on personal observations of the genitalia, where the Blattellidae and Blaberidae have more morphological similarity to each other than to the Polyphaginae. The latter show more affinities with the Blattidae. The closeness of the Epilamprinae to the panchloroins in models (see Figs. 46 and 49) of the author's data also supports these arrangements. The data for the blaberoins is not sufficient to permit a choice between 1A and 2A.

The correlation phenogram (Fig. 2) computed from McKittrick's Table 1 agrees well with Figures 1 and 4 except for the emergence of the Polyphaginae with the blattoids rather than the Blattellidae. However, the Lamproblattinae, Cryptocercinae, Polyzosteriinae and Blattinae all rank before the Blattellidae in the column Polyphaginae. This placement of the Polyphaginae is confirmed by both subjective and objective observation of the genitalia. The discrepancy between McKittrick's phyletic and the calculated phenetic data indicates that an investigation of the Polyphagidae would be profitable. McKittrick was able to sample only a few polyphagids and Roth (1967b) calls for further study of this family. It was unfortunate that the other polyphagid subfamily, the Holocompsinae, was unobtainable for the present study, for McKittrick's illustrations and description of the genitalia of a holocompsine suggests more similarity to the Blattellidae than is shown by the Polyphaginae. A study of correlations, using all of the original OTU's of McKittrick's Table 1 (Huber, unpubl.), shows that the Holocompsinae are closest to the Polyphaginae, followed by the blattoids. It is interesting to note that the Holocompsinae are closer to the nearest blattellid than are the Polyphaginae:

OTU's	r
Polyphaginae—Anaplectinae	0.076
Holocompsinae—Anaplectinae	0.249

Further study of Figure 2 shows that the resolving power of the characters used is insufficient to separate the Polyzosteriinae from the Blattinae. The Lamproblattinae and the Cryptocercinae rank highest in these two columns and the Lamproblattinae rank second in the column Cryptocercinae.

The Plectopterinae and Blattellinae pair in each other's columns, but are much less similar than any other subfamilies within a single family. The Blaberidae show several completely correlated ($r = 1.00$) OTU's and do not reflect the phylogram (Fig. 1) at all. McKittrick uses additional data (her Tables 6 and 7) to separate these subfamilies.

The Cryptocercidae and Blattidae have identical first and second axis projections in the model (Fig. 3) and differ only along the third. The Polyphaginae are near the blattoids. The Cryptocercinae rank highest in the column Polyphaginae, followed by the Blattidae, Blaberidae and Blattellidae, respectively. The Blattidae are second in rank in the column Cryptocercinae. McKittrick places the Polyphaginae (which she regards as primitive blaberoids) with the Blaberoidea rather than the Blattoidea. The actual position of the Polyphaginae is better shown in the model (Fig. 3) than in the phenogram (Fig. 2). While in Figure 3 this subfamily is closer to the Blattoidea than to other Blaberoidea, note that it does not have the same projection as the blattoids on the first, second or third axes, suggesting that

there is some fundamental difference between the Polyphaginae and the Blattoidea.

The primitive form of rotation of the ootheca found in certain Polyphagidae (Roth, 1967b) separates this group from the blattoids. Perhaps we can regard this as a preadaptive state of the more advanced type of rotation of the other blaberoids, which would place the polyphagids at the stem of blaberoid evolution, at the point where the group was able to invade a new adaptive zone. Thus Figure 3, which was derived by computation, is comparable with McKittrick's phyletic tree (Fig. 1). By merely drawing lines between the clusters and indicating the presumed direction of evolution, Figure 3 can be converted into a 3-dimensional version of Figure 1.

Large gaps are present between families and much smaller ones between subfamilies in the three-dimensional model (Fig. 3). In the present study, families are not as clearly defined in the models and phenograms (Figs. 32-49) as they are in Figures 2 and 3 based on McKittrick's results with adults. Figures 46 and 49, however, which are also based on adults, do show more discrete family grouping than the models of the nymphal stages. Gaps between the complexes and most subfamilies can be seen in all the models of the present study, but the Blattidae are clearly defined only in those of the adult OTU's. The Blattellidae do not divide into subfamilies in any model (though this can be seen in the correlation phenogram of the adult males [Fig. 47]).

The phenetic approach, as in this study, uses large numbers of virtually unselected characters and does not produce such clear-cut results as conventional phyletic methods. However, distortion of relationships may be produced if the object of a phyletic classification is merely to produce differentiation between taxa. Phenetic methods can provide new dimensions (for example, the effects of ecological adaptation) in an analysis of the affinities within a group.

4.2. McKittrick's Table 2: Female genitalia in the Cryptocercidae and Blattidae

Species are the OTU's in this and all succeeding parts of Section 4. The six corresponding to those of the present study are the only ones used. Thirty-two out of 33 condensed characters actually varied and are used in the computations.

McKittrick summarizes findings from her Tables 2 and 3 in a phylogram (Fig. 5). The interpretive phenogram (Fig. 6) shows only a weak cophenetic correlation ($r = 0.603$, presumably significantly different from zero) with the matrix of correlations derived from McKittrick's Table 2. The main difference between the interpretive and computed (Fig. 7) phenograms is in the placement of *Cryptocercus punctulatus*. In Figure 6 it is the last to join the phenogram, while in Figure 7 *Lamproblatta albipalpus* and *C. punctulatus* pair before joining the other OTU's. The two blattines, *Periplaneta americana* and *Blatta orientalis*, also pair and, in both columns, *L. albipalpus* ranks third. *Eurycotis floridana* ranks higher in both these columns than *Platyzosteria melanaria*. The polyzosteriines also form a pair. The distance phenogram and Figure 7 have the same sequence of branchings.

The centroid component model (Fig. 8) shows distinct constellations, identical with the clusters of the correlation phenogram (Fig. 7). *C. punctulatus* is sufficiently isolated from *L. albipalpus* so that they are not mutually closest. *L. albipalpus* is second in the column *C. punctulatus*, and *B. orientalis* ranks highest in the column *L. albipalpus*. *B. orientalis* and *Periplaneta americana* are mutually closest and *L. albipalpus* ranks third in both columns. *E. floridana* and *Platy-*

zosteria melanaria are also mutually closest, but *E. floridana* is nearer than *P. melanaria* to the blattines.

Discussion of these results is postponed until McKittrick's Table 3 has been analyzed, since it concerns the same OTU's.

4.3. McKittrick's Table 3: Proventricular characters in the Cryptocercidae and Blattidae

Of 30 condensed characters in the data matrix, only 24 varied among OTU's. The OTU's are identical with those in McKittrick's Table 2, so the same phylogram (Fig. 5) and interpretive phenogram (Fig. 6) apply. The cophenetic correlation with the matrix of correlations derived from McKittrick's Table 3 is even weaker ($r = 0.458$) than the one from her Table 2 and is presumably not significantly different from zero.

The correlation phenogram (Fig. 9) differs from the interpretive phenogram (Fig. 6). In the former *C. punctulatus* and *L. albipalpus* pair and *Platyzosteria melanaria* ranks third in both columns. *Periplaneta americana* and *E. floridana* also pair and rank highest in the column *B. orientalis*. Finally, *B. orientalis* and *C. punctulatus* are closest in the column *Platyzosteria melanaria*. The distance phenogram shows the same sequence of branchings.

The constellations in the centroid component model (Fig. 10) correspond to the clusters of the correlation phenogram (Fig. 9). Unlike Figure 8, in Figure 10 *E. floridana* clusters with the blattines and *L. albipalpus* is between *C. punctulatus* and the constellation *Periplaneta americana, B. orientalis* and *E. floridana*. *P. americana* and *B. orientalis* are mutually closest to each other.

The association between *C. punctulatus* and *L. albipalpus* suggests that the former should be classified with the Blattidae. *C. punctulatus* clusters with *L. albipalpus* in Figures 2 and 7 and they are close in the models (Figs. 8, 10). In my small nymph models (Figs. 34, 37) *C. punctulatus* is closest to the Blattidae, but in the large nymph (Figs. 40, 43) and the adult models (Figs. 46, 49) it is progressively further removed from this family. However, in the adults and large nymphs it is closer to *L. albipalpus* than to any other blattid. McKittrick (1964, 1965) has been influenced by other data not included in her tables, but which she reviews in detail. She finds that the characteristics which are common to *C. punctulatus* and *L. albipalpus* are not the same as the many features shared by *C. punctulatus* and *Mastotermes*. Because of this she separates *Cryptocercus* from the Blattidae. I would agree with this decision. Unfortunately the Polyphagidae are omitted from McKittrick's Tables 2 and 3, for it would be most instructive to make a comparison between this family and the blattoid OTU's using the same characters. However, she concludes elsewhere (1965) that despite similarities between the genitalia of certain polyphagids and *Cryptocercus*, the differences indicate that the Polyphagidae really diverge from the blattoid families. This is supported by, among other things, the basic structural differences in the proventriculus (cf. discussion of McKittrick's Table 1).

Eurycotis floridana is in a different position in the analyses of McKittrick's Tables 2 and 3. The female genital characters are polyzosteriine, while in the proventricular characters *E. floridana* is (or remains, phyletically speaking) blattine. These results are still true when all of McKittrick's OTU's in Tables 2 and 3, including a second species, *E. pluto* Hebard, are analyzed (correlation and distance phenograms only, Huber, unpubl.). Male genital characters (Huber, unpubl.) produce the following results. In the correlation phenogram, adult male *E.*

floridana and *Platyzosteria melanaria* cluster together but do not pair and are distinct from the blattines, while in the distance phenogram, these two OTU's do not cluster together but neither do they cluster with the blattines. McKittrick (1964:20-21, and my Fig. 5) suggests that *E. floridana* is intermediate between the Blattinae and Polyzosteriinae, but finally places this genus in the latter subfamily. I am not certain I can agree with her decision. This might be an example of mosaic evolution in a genus which should belong to two subfamilies simultaneously, a procedure suggested by Michener (1963) in cases where an OTU is intermediate between two clusters.

Models based on my data show the subfamily structure proposed by McKittrick. It is less clear in the small nymphs, but becomes progressively more defined in the large nymphs and adults.

4.4. McKittrick's Table 4: Male and female genitalia in the Polyphagidae and Blattellidae

There are six OTU's and 30 varying characters (remaining from a condensed 37) in this data matrix. McKittrick summarizes the groups within the Polyphagidae and Blattellidae in a phylogram (Fig. 11) and an interpretive phenogram (Fig. 12) has been drawn from this. The cophenetic correlation between the similarity values extracted from this phenogram and the matrix of correlation coefficients computed from the Table is 0.740 (presumably significantly different from zero). The interpretive (Fig. 12), correlation (Fig. 13) and distance (Fig. 14) phenograms agree well with each other and with McKittrick's classification. The exception is *Arenivaga bolliana*. In Figure 13 this OTU is closer to the Plectopterinae than in the phylogram (Fig. 11) and cannot be separated from the Blattellidae by any straight phenon line.

The three-dimensional model (Fig. 15) constructed from these data shows the same relationships as the distance phenogram (Fig. 14). The constellations formed by the Plectopterinae and Blattellinae are closer to each other than either is to *A. bolliana*. *Lophoblatta fissa* and *Supella longipalpa* are widely separated and these two species rank highest in the column *A. bolliana*.

In the two distance matrices, *S. longipalpa* is closer than *L. fissa* to the nearest blattelline. This is not so in the correlation matrix, where the situation is reversed.

I suggest that the Polyphaginae are phenetically blattoid rather than blaberoid, but analysis of McKittrick's Table 4 shows a close similarity between *A. bolliana* and the Plectopterinae.

4.5. McKittrick's Table 5: Proventricular characters in the Blattellidae

McKittrick uses the same OTU's as Table 4, omitting *A. bolliana*. Only 16 vary out of 27 condensed characters. The cophenetic correlation between the similarity matrix derived from the interpretive phenogram (Fig. 12, excluding *A. bolliana*) and the correlation matrix calculated from McKittrick's Table 5 is 0.884 (presumably significantly different from zero).

The correlation phenogram (Fig. 16) has plectopterine and blattelline branches, but the blattelline OTU's are not sorted out by the characters used. In Figure 16, *S. longipalpa* is closer than *L. fissa* to the blattellines and it clusters with them in the distance phenogram (Fig. 17).

The model (Fig. 18), constructed from the centroid component analysis, shows that the Blattellinae are completely correlated and occupy a single point on the model. *S. longipalpa* is again closer than *L. fissa*.

S. longipalpa is usually closer than *L.*

fissa to the blattellines in the analyzed data from McKittrick's Tables 4 and 5 and in the models of large nymphs and adults (Figs. 40, 43, 46, 49), but not in those of the small nymphs (Figs. 34, 37). Subfamily divisions are not as clearly defined in models and phenograms from my study (Figs. 32-49) as they are in those of McKittrick (Figs. 11-18).

4.6. McKittrick's Table 6: Female genitalia in the Blaberidae

This data matrix has 15 OTU's and 30 of 31 condensed characters. McKittrick summarizes her views on the taxonomy of the Blaberidae in phylograms (Figs. 1, 19, 20). In Figure 1 the epilamproins are placed between the other two complexes and apparently not aligned with either.

The interpretive phenograms (1, 1A, 1B, 2, 2A, 2B) were tested for correlation with the correlation matrix derived from the data. In all schemes 1, the epilamproin cluster joins the blaberoin cluster first. In all schemes 2, the epilamproin cluster joins the panchloroin cluster first. Other differences are:

1, 2. *Panesthia angustipennis* clusters with *Eublaberus posticus—Byrsotria fumigata. Archimandrita tesselata—Blaberus,* followed by *Phortioeca phoraspoides,* then join.

1A, 2A. These resemble the above, but *P. angustipennis* joins the united couplets *B. fumigata—E. posticus* and *A. tessellata —Blaberus* before *P. phoraspoides.*

1B, 2B. These are like the first two, but *P. phoraspoides* joins *B. fumigata—E. posticus* and *A. tessellata—Blaberus* before *P. angustipennis* is added.

The resulting cophenetic correlations range from 0.696 to 0.778. All are presumed significantly different from zero. The extreme values are close enough to suggest a homogeneous group of coefficients. Therefore, of the six arrangements, scheme 1 was arbitrarily chosen for illustration (Fig. 21, $r_{coph} = 0.756$).

In the correlation phenogram (Fig. 22) all OTU's within a subfamily join together before making other connections. The epilamprines join the Blaberinae and Panesthiinae (blaberoins) while the remaining blaberoin subfamily (Zetoborinae) joins the Oxyhaloinae. The other panchloroin subfamilies cluster together. These relationships are similar to those observed in the models of my data, especially in the adults (Figs. 46, 49). In column *Phortioeca phoraspoides, Panchlora nivea* is second and no blaberoins are encountered until *Panesthia angustipennis* (eighth). The nearest blaberine is *Blaberus discoidalis* which is in 12th place. In the *P. angustipennis* column, *E. posticus, B. discoidalis* and *B. fumigata* rank closest. In the column *Audreia cicatricosa, Hyporhicnoda litomorpha* and *B. discoidalis* have the highest correlations. *B. discoidalis* and *A. cicatricosa* rank second and third in column *H. litomorpha.*

In the distance phenogram (Fig. 23), the Zetoborinae and Panesthiinae are the last two subfamilies to join. The Blaberinae annex each epilamprine separately. *Pycnoscelus—Capucina patula* is identical to the corresponding cluster in Figure 22. In the three-dimensional model (Fig. 24), the Blaberinae form a short linear constellation. *Panesthia angustipennis* is near one end and *Phortioeca phoraspoides* is at the other end somewhat removed from the blaberines so that the blaberoins are arranged in an elongate, curved line. The panchloroins are arranged about a line, beginning under the blaberoins (underneath *P. phoraspoides*) and rising to the more isolated oxyhaloine constellation. *A. cicatricosa* and *Gromphadorhina portentosa* are nearest in column *P. phoraspoides.* The two epilamprines are mutually closest to each other and both rank *B. discoidalis* third.

The general impression of phenetic relationships in the model (Fig. 24) is that

they are not too different from those seen in the models of my study, especially those of the adults (Figs. 46, 49). The model illustrates McKittrick's contention (1964: 34) that the Blaberinae are intermediate between the Zetoborinae and Panesthiinae. These two are much closer together in my adult male model (Fig. 49) than in Figure 24, and still closer in the adult female (Fig. 46), but in neither case are they separated by the Blaberinae. In my adult models, the Epilamprinae are, in general, closest to the panchloroins, while in Figure 24 they are clearly nearest the blaberoins. The models of my study (Figs. 34, 37, 40, 43, 46, 49) show the Oxyhaloinae at the intersection of the two complexes while in Figure 24 they are distant from it. The oxyhaloines are widely dispersed in all the models of my study, but in Figure 24 (female genital characters) and in male genital characters (Huber, unpubl.) they form a single constellation. These discrepancies are the result of different suites of characters used in these studies.

4.7. McKittrick's Table 7: Proventricular characters in the Blaberidae

McKittrick's Table 7 includes the same OTU's as her Table 6 except that *Blaberus giganteus* replaces *B. discoidalis*. Thirty-three of the condensed 36 characters vary among these OTU's. The interpretive phenograms described in Section 4.6 were compared with the correlation matrix from McKittrick's Table 7. The cophenetic correlations are much weaker than those found in Section 4.6, ranging from 0.411 to 0.476, presumably not significantly different from zero but appearing to form a homogeneous group of coefficients. The magnitude of the difference between the lowest cophenetic correlation from McKittrick's Table 6 (0.696) and the highest from her Table 7 (0.476) suggests that the two groups of coefficients are not members of the same population. Since the same interpretive phenograms are used in both cases, the interrelationships implied by the data in these two tables must differ in important respects from each other. Thus, the relationships shown in the correlation phenogram (Fig. 25) bear little similarity to those of Figure 22. In the distance phenogram (Fig. 26), *Phortioeca phoraspoides* is the last OTU to join. *Panchlora nivea* and *C. patula* rank nearest in column *P. phoraspoides*. *Pycnoscelus* and *H. litomorpha* pair, with *Archimandrita tessellata* third in the former and *Diploptera punctata* third in the latter column. The column *Audreia cicatricosa* ranks *H. litomorpha* and *Pycnoscelus* second and third. *Nauphoeta cinerea* is second in column *P. nivea,* and the other panchlorine, *C. patula,* is tenth. In column *C. patula, G. portentosa* and *P. nivea* rank second and seventh, respectively.

Examination of models and phenograms resulting from an analysis of McKittrick's tables shows that she was more influenced by the genital data (Table 6) than by the proventricular data (Table 7) in constructing her classification. At first glance, the model and phenograms (Figs. 25-27) based on her Table 7 do not closely resemble her classification. However, the proventricular characters were useful to McKittrick (1964:113) for showing more clearly certain trends and subfamily groupings. For example, Figure 27 shows better differentiation among the members of the panchloroin complex than does Figure 24 (based on her Table 6).

When the OTU's of each of the complexes are examined separately on the model (Fig. 27), their phenetic relationships are very similar to those of Figure 24. Among the blaberoids, *A. tessellata* and *B. giganteus* are centrally located, with *E. posticus, B. fumigata* and *Panesthia angustipennis* on one side and *Phor-*

tioeca phoraspoides on the other. This is precisely what McKittrick's phylogram, Figure 19, shows. If the panchloroin OTU's in Figure 27 are considered separately, the sequence is: Panchlorinae, Oxyhaloinae, *D. punctata, Pycnoscelus.* The Oxyhaloinae are somewhat removed from the line formed by the other OTU's. In Figure 24, they are also isolated but beyond *Pycnoscelus.* My adult models (Figs. 46, 49) show in the following order: *C. patula,* with the centroid of the oxyhaloines beside it, *D. punctata* closely associated with the Pycnosceli, *Panchlora nivea. P. nivea* is not as close to *C. patula* as one would expect, probably because of the difference in size between the two species. Much the same sequence is found in the nymphal models (Figs. 34, 37, 40, 43). (*D. punctata* is displaced in the small nymph models and phenograms, but this is discussed later, in Section 6.2.1.) The sequences in Figures 46 and 49 correspond exactly with that of Figure 27. Thus there is considerable agreement between McKittrick's Table 7 (and 6, excluding the Oxyhaloinae) and the models constructed from my data. It is not clear why the blaberoins *A. tessellata* and *B. giganteus* should emerge in the midst of the panchloroin series in Figure 27. This situation obviously calls for further study.

The incongruence of the position of the Oxyhaloinae in Figure 24 compared with Figure 27 points to the need for increased understanding of these character complexes. The recoding of characters and the use of some new ones could produce a reconciliation of the phenetic position of this subfamily in the two models or, on the other hand, it could demonstrate that this is a case of mosaic evolution.

Study of her Tables 6 and 7 enables us to appreciate McKittrick's uncertainty about the relationships among the three blaberid complexes. In Figure 24 the epilamproins are clearly closer to the blaberoins, but in Figure 27 they are closest to the panchloroin *Pycnoscelus.* In the adult female model (Fig. 46), the epilamproins *H. litomorpha* and *Audreia bromeliadarum* are close to the blaberoin *Panesthia australis,* considerably separated from the panchloroins and at an even greater distance from the other blaberoins. In the adult male model (Fig. 49), both epilamproins are unquestionably closer to the panchloroins. A correlation phenogram using male genital characters from my own data (Huber, unpubl.) shows *A. bromeliadarum* joining with a panchloroin cluster and *H. litomorpha* uniting first with *Panesthia australis* and then joining a cluster composed of blaberoins and panchloroins. Further investigation would certainly be profitable since the affinities within the Blaberidae differ according to which set of characters is used.

McKittrick (1964:110) regards the male genitalia of the Blaberidae as too similar in appearance to be a useful taxonomic tool. However, I have found this not to be so in my phenograms of male genital characters (Huber, unpubl.). These show that even apparently uniform structures may still provide valuable taxonomic information but that a numerical method of evaluation is necessary to use the extracted data to their fullest advantage.

5. COMPARISONS AMONG TWO CLASSIFICATIONS OF BLATTARIA AND THAT OF McKITTRICK

McKittrick's classification is compared with two others based on the combined OTU's (Section 2.3) of my data. My classification produced from the combined adult OTU's corresponds more closely in its source of material to McKittrick's classification since she used only adult specimens. Sokal and Sneath (1963), however, believe that it is important to use all available characters. Thus my second

classification uses combined OTU's of all stages.

Construction of centroid component models would have greatly aided in evaluating the correlation and distance phenograms. But the number of characters in both data matrices far exceeds the capabilities of the computers available to me. Since no impartial method of selecting approximately 300 characters from the data matrix could be decided on, factor analyses were not performed.

5.1. Classification of Blattaria using combined adult characters

The families of McKittrick emerge in my phenograms (Figs. 28, 29), but not with the distinctness seen in Figures 2 to 4.

As in all phenograms derived from my data, the Blaberidae are split into two groups, a cluster including all the larger species, the blaberines and *Leucophaea maderae,* and another containing the smaller forms. *Blaberus craniifer, Blaberus discoidalis* and *Blaberus giganteus* cluster together in Figures 28 and 29. In the distance phenogram (Fig. 29), the larger and smaller blaberids join to form a single cluster but exclude *A. bromeliadarum, Panesthia australis* and *G. portentosa.* In the correlation phenogram (Fig. 28), the two major clusters are widely separated. The larger blaberids join blattids and only the smaller ones mirror McKittrick's scheme by uniting with the Blattellidae. The Panchlorinae *Panchlora nivea* and *C. patula* do not cluster together. The Oxyhaloinae are widely separated and so are the epilamprines. The blaberoin *Phortioeca phoraspoides* clusters with the smaller blaberids (panchloroins) in both phenograms in the same manner as in the correlation phenograms (Figs. 22, 25) of McKittrick's Tables 6 and 7. Its displacement is emphasized in the distance phenograms of McKittrick's data (Figs. 23, 26) where it is not only isolated from the other blaberoins but is the last OTU to join the entire cluster.

The Blattidae cluster together in both phenograms. In Figure 29, the distance phenogram, each subfamily forms a separate subcluster. The joining of the Polyzosteriinae with the Lamproblattinae is at variance with McKittrick but is probably explained by the apterous or brachypterous condition of these OTU's. The latter wing condition is also present in the female of *Blatta orientalis,* which may provide a reason for its clustering with *E. floridana - L. albipalpus* in the correlation phenogram (Fig. 28) instead of with the other Blattinae.

The polyphagid *Polyphaga saussurei* is annexed by the blattid cluster in Figure 29 but not in the correlation phenogram (Fig. 28) where it joins *C. punctulatus - P. saussurei,* a cluster composed of other aberrant large forms belonging to several families. In the correlation matrix, however, column *Polyphaga saussurei* ranks *Arenivaga erratica* and *Platyzosteria melanaria* second and third, while *Attaphila fungicola* and *P. saussurei* are closest in column *A. erratica.* The polyphagids also rank high in each other's columns in the distance matrix. *A. erratica* joins with *A. fungicola* and then they both cluster with Blattellidae in both phenograms in conformity with McKittrick's classification. Thus the polyphagids are closer to each other than would appear from their position in the phenograms.

C. punctulatus pairs with *Panesthia australis* in what McKittrick has described as an extraordinary case of convergence, since *C. punctulatus* is regarded as primitive, while *P. australis* belongs to one of the most highly evolved families. These two OTU's are placed in their presumably correct cladistic positions only in the small nymph classifications (Section 6.2.1), though the nature of their phenetic rela-

tionship may be appreciated in the models of all stages.

In the correlation phenogram (Fig. 28), *Ischnoptera deropeltiformis* and *A. fungicola* do not cluster with the Blatellidae. The other blattellids fall into two clusters which correspond to the subfamilies of McKittrick. *L. fissa* and *A. fungicola* are excluded from the family cluster in the distance phenogram (Fig. 29). The remaining blattellids form a single cluster but McKittrick's subfamilies are not defined.

5.2. Classification of Blattaria using combined characters from all stages

In the phenograms (Figs. 30, 31), the Blaberidae are again divided. One cluster includes the larger forms, the Blaberinae. *L. maderae* joins the cluster in the correlation phenogram (Fig. 30) and *H. litomorpha* and *Phortioeca phoraspoides* in the distance phenogram (Fig. 31). *Blaberus* does not remain intact in either phenogram. The smaller blaberids are close to the Blattellidae in both phenograms which is in accordance with McKittrick. The individual members of the Oxyhaloinae, Panchlorinae and Epilamprinae are dispersed.

The larger blaberids in Figure 30 cluster with a varied group of large and, in some stages, heavy-bodied OTU's (*C. punctulatus - H. litomorpha*). Most of the latter are "late-joiners" in the distance phenogram (Fig. 31), a sign of their aberrant nature. One of these is the polyphagid *Polyphaga saussurei*. The other polyphagid, *A. erratica,* joins with the blattellid *A. fungicola* and together they cluster with the Blattellidae in Figure 30 as McKittrick arranges them. But as in Section 5.1, the polyphagids are closer together than the phenograms indicate, for *P. saussurei* is third in column *A. erratica* and *A. erratica* is second in column *P. saussurei*.

C. punctulatus and *Panesthia australis* cluster together in both phenograms, but pair only in the correlation matrix. In the distance matrix, *L. albipalpus* is highest ranked in column *C. punctulatus* while *P. australis* is sixth. In column *P. australis, D. punctata* is second and *C. punctulatus* is fifth. Thus the relationships of these two OTU's are cladistically more accurate in the matrices when nymphal characters are added to adult characters (cf. Section 5.1).

Most of the Blattellidae form a cluster by the fusion of blattellines and plectopterines in Figure 30. In the distance phenogram (Fig. 31) the subfamilies are not distinct, though the plectopterine *S. longipalpa* is the last to join the blattelline cluster *Blattella germanica - Parcoblatta pensylvanica. I. deropeltiformis, L. fissa* and *A. fungicola* are scattered and separated from the other blattellids. But the blattelline *Symploce hospes* is closest in column *I. deropeltiformis* in both matrices. The isolation of the latter from its family is treated more fully later.

Although the Blattidae cluster together, the subfamily arrangement of McKittrick is not accurately shown in either phenogram. The Blattinae form a single group in both phenograms, but *B. orientalis* and *Periplaneta americana* pair leaving the remaining Periplanetae to form a cluster. The two polyzosteriines *Platyzosteria melanaria* and *E. floridana* do not cluster but join with *L. albipalpus,* a lamproblattine, probably because all three OTU's are brachypterous or apterous as adults. McKittrick does not regard these two subfamilies as closely related.

6. OTHER CLASSIFICATIONS OF THE PRESENT STUDY

6.1. Cophenetic correlations among matrices

With one exception, the highest cophenetic correlation coefficient is between the

similarity matrices of the adults and large nymphs of both sexes (Tables 6, 7, 10). The small nymph matrix is more similar to that of the large nymph than to the adult. This is the case for all three measures of similarity: coefficients of correlation, distance, and centroid distance. Superficially, it is the large and small nymphs which most resemble each other. I would conclude therefore that the adult differentiations must already be present and measurable in the large nymphs. It should be emphasized that the similarities are an expression of interrelationships and not of anatomical structures. The exception mentioned above occurs among the centroid distances for the males where the r_{coph} for adults - small nymphs is higher than for large nymphs - small nymphs (Table 10). The reason for this anomaly is not clear.

A cophenetic correlation represents an average value for all coefficients in two matrices. It would be interesting to study similarity coefficients among the six OTU's within a single species, especially one with wingless adults. The relationships could be quite different from those described above.

When comparisons between sexes of the same instar are made (Tables 8, 9, 11), the three similarity coefficients again give like results. The matrices of the male and female small nymphs are most similar, those of large nymphs are intermediate and those of adults are least similar to each other. This progression reflects the increasing morphological differentiation and divergence between the sexes from hatching to maturity. This phenomenon is not due entirely to the presence of complex alary and genital structures in the adults, for the centroid distance coefficients are based on characters with either one or no NC's. This has the effect of deleting many wing and genital characters. The centroid component analyses retain only 6 of 62 (10%) wing characters. For the adult females, 29 out of 50 (58%) and for adult males, 17 out of 76 (22%) of the genital characters remain. Nevertheless the cophenetic correlations of centroid distances (Tables 10, 11) follow the same pattern as the matrix comparisons among correlation and distance matrices (Tables 6-9). The divergence of the adult classifications must be partly due to differentiation of structures other than genitalia and wings, though many of the remaining genital characters have high communalities and thus must be influential in determining the positions of OTU's on the model.

When matrices are compared among instars and between sexes (Tables 8, 9, 11), the same general pattern first noted recurs, namely, that adults - large nymphs are most similar, followed by small nymphs - large nymphs. We find one exception in the matrix of correlations derived from centroid distances (Table 11), where the correlation between small nymph females - adult males is slightly higher than small nymph females - large nymph males. The reason for this deviation is not apparent.

6.2. Comparison of classifications of the sexes at each ontogenetic stage

6.2.1. Small nymphs: Considerable interdigitation of family boundaries is seen in the small nymph models (Figs. 34, 37) and in the "mixed" clusters of the phenograms (Figs. 32, 33, 35, 36). This indicates possible ecological similarities among members of different families as measured by morphological criteria. The mixed group in the models includes small nymphs of *B. orientalis, L. albipalpus* and *Periplaneta americana* (Blattidae); *C. punctulatus* (Cryptocercidae); *N. cinerea, Pycnoscelus indicus* and *Pycnoscelus surinamensis* (Blaberidae); and *Parcoblatta pensylvanica* (Blattellidae). Nevertheless,

the majority of other small nymph OTU's cluster most closely with their families.

The distribution of Blaberidae in the phenograms is clarified by study of the models where the OTU's of the blaberoin and panchloroin complexes form intersecting lines. The Blaberinae are isolated at the end of the blaberoin line in both models because of their larger size. They form distinct and isolated clusters in the phenograms. *G. portentosa* (a panchloroin) joins them in the correlation phenograms (Figs. 32, 35) and is the last to join the distance phenograms (Figs. 33, 36). *L. maderae* also clusters with the blaberines in the phenograms and is near them in the models. The proximity of the Oxyhaloinae to the blaberoins is at least partly due to their size (larger than the other panchloroins). It may also be an indication of their closeness, in the cladistic sense, to the blaberoins; McKittrick (my Fig. 1) shows this as the first subfamily to branch off the panchloroin stem.

Another effect of size is seen in the phenograms. Here *D. punctata* clusters with the blaberines instead of the panchloroins as would be expected from McKittrick. However, *D. punctata* is three times larger at hatching than the small nymph of, say, *Panchlora nivea* and yet the adults are of comparable size. Roth and Hahn (1964, esp. their Fig. 3) illustrate this considerable difference in size between newly emerged *D. punctata* and *N. cinerea*. The latter species even has larger adults than *D. punctata*. Willis, Riser and Roth (1958) point out that *D. punctata* undergoes only four molts to reach maturity, compared with the usual 7 to 13 in a sample of 11 other species of Blattaria. It is most likely that the small number of instars can be correlated with the large size at hatching. It should also be noted that *D. punctata* receives nourishment from the mother while being carried in the brood sac (Roth and Willis, 1955a). It is possible that it is the first few molts that have been eliminated. Thus a first instar *D. punctata* may not be comparable in its anatomy to other first instar cockroaches. This may explain the anomalous position of *D. punctata* in the phenograms.

The panchloroin OTU's extend from *Panchlora nivea* to *G. portentosa* (Figs. 34, 37). In the females, small nymphs *D. punctata, L. maderae* and *G. portentosa* are displaced (Fig. 34) while only *L. maderae* is displaced in the male model (Fig. 37). Small nymph male *Panesthia australis* lies at the intersection, while the female is not on either line. In spite of this difference, both sexes of small nymph *Panesthia australis* are always closest to panchloroins in all the small nymph matrices and bear no close similarity to *C. punctulatus* as they do in the adults.

The Oxyhaloinae are widely dispersed in the models and phenograms. The greatest distances between these OTU's in the models are along the first axis, in which size is important. Their spread along the second axis is less than that seen among the three Blaberi. In contrast, the oxyhaloines form compact clusters when proventricular or genital characters are considered (Figs. 21-27).

The Blattellidae form a compact constellation in the models except for *Parcoblatta pensylvanica* which has a high enough projection on the first axis to place it in the mixed group. Size alone cannot account for this displacement because both sexes of small nymph *Blattella vaga* have lower first axis projections but are actually slightly larger OTU's than *Parcoblatta pensylvanica*. Separation into the subfamilies of McKittrick is not evident in either models or phenograms. *S. longipalpa* is isolated from the other blattellids and clusters with them in only one instance (Fig. 35).

In all three small nymph female simi-

larity matrices, *B. orientalis* ranks highest in column *Polyphaga saussurei*. Figure 34 shows the small nymph female *P. saussurei* on the edge of a band of Blattidae which crosses the model parallel to the second axis. But *P. saussurei* has a higher third axis projection than any blattid. I regard this as independent confirmation of my phenetic placement of the Polyphaginae discussed previously, because it is based on an entirely different suite of characters.

The small nymph female *Cryptocercus punctulatus,* regarded by McKittrick (1964, 1965) as representing the most primitive living cockroach, occupies a central position in phenetic hyperspace as shown by its position in the mixed constellation (Fig. 34). This may reflect its generalized morphology. In all three small nymph female matrices, a blattellid ranks highest in column *C. punctulatus*. In Figure 37, small nymph male *C. punctulatus* is at the edge of the mixed group and in all three matrices a blattid ranks second in its column. In both sexes, the position of *C. punctulatus* in the models shows it to be close to the Blattidae, with which it is grouped by McKittrick. In the large nymph and adult phenograms, *C. punctulatus* shows extreme "convergence" with *Panesthia australis* (cf. McKittrick, 1964, 1965), and only in the small nymph models and phenograms of both sexes does it show a phenetic position comparable to its cladistic one. The interesting fact, not previously reported, that both sexes of small nymph *C. punctulatus* lack compound eyes has apparently not had much effect on their placement.

The most striking difference between the models for the two sexes is in the arrangement of the Blattidae. *Eurycotis floridana, Platyzosteria melanaria, Periplaneta brunnea, Periplaneta fuliginosa,* and *Periplaneta australasiae* change polarity on the second axis from positive in the female to negative in the male (Figs. 34, 37). The remaining blattids retain approximately the same relative positions. *Periplaneta fuliginosa, Periplaneta australasiae, Periplaneta brunnea,* and *Platyzosteria melanaria* form a cluster in all small nymph models and phenograms cutting across the subfamily divisions of McKittrick's classification. Small nymph male *E. floridana* clusters with them in Figures 35 and 36, but the female is too isolated for this. In contrast to the relationships shown in the models (Figs. 34, 37), McKittrick considers *E. floridana* to be closer (phyletically, see Fig. 5) to the Blattinae than is *Platyzosteria melanaria*. Since *E. floridana* is considerably larger than *P. melanaria,* which, in turn, is approximately the same size as the Periplanetae, the isolation of the former is due only to its large size in this instar. Therefore, I conclude that there is no justification for separation of Blattinae from Polyzosteriinae in the small nymphs.

The remaining blattines, *Periplaneta americana* and *B. orientalis,* are isolated from the rest of the subfamily. It is not clear why. *P. americana* does not differ in any obvious respect from its congeners. *B. orientalis* is an unexceptional blattine in the organ systems considered by McKittrick, but the adults are brachypterous which serves to differentiate this species from the others in the subfamily. *L. albipalpus* lies between the *P. americana* - *B. orientalis* and Periplanetae - *Platyzosteria melanaria* constellations (Figs. 34, 37). This may indicate that it is a generalized as well as a primitive blattid.

The models show how the blaberid, blattellid and blattoid distributions intersect in the first three dimensions. Their behavior in higher dimensions is not known but would be interesting to investigate. The phenetic similarities among these families cannot at the present time be decomposed into patristic and homo-

plastic components (Sokal and Camin, 1965) because of insufficient knowledge of the exact nature of the color, pattern and size characters.

6.2.2. Large nymphs: The models of large nymphs of both sexes (Figs. 40, 43) appear similar. The most striking feature of the distribution of the Blaberidae is that the strings of blaberoins and panchloroins are still present and intersect as in small nymphs. The blaberoins include *Panesthia australis,* but in both sexes this OTU is far from the Blaberinae and lies closer to the panchloroins. In both cases, *L. maderae* is on the blaberoin line and remote from the panchloroins. In general, the panchloroins form a line in the males (Fig. 43) and a band in the females (Fig. 40). In the models, the only oxyhaloine close to the other panchloroins is *N. cinerea.* It also clusters with them in the phenograms (Figs. 38, 39, 41, 42). In these Figures, *L. maderae* and *G. portentosa* cluster with the blaberoins except for the large nymph female *G. portentosa* (Fig. 39). The centroid of the three oxyhaloines is closer than any other panchloroin OTU to the blaberoin line. This arrangement is in accord with McKittrick's views (Fig. 1). *L. maderae* is actually the closest oxyhaloine to the blaberoins. This must be because of a phenetic resemblance, not larger size alone, because this relationship does not change even if size is disregarded (by consideration of only the second axis projections). It is interesting to note that most of the variation among the panchloroin OTU's is along the first axis and is thus attributable to size, whereas among the blaberoins more of the variation is along the second axis representing other, not yet interpreted, factors.

In the correlation phenogram for the large nymph females (Fig. 38), *G. portentosa* clusters with *Polyphaga saussurei.* The models (Figs. 40, 43) show these OTU's and *Panesthia australis* occupying isolated positions in the fourth quadrant of the first two axes. In spite of their relative phenetic nearness, these three are not close enough to form a constellation of points in the models (Figs. 40, 43). Evidently they are influenced by their presumed phyletic history since *Panesthia australis* is at the end of the blaberoin line (Fig. 40), *G. portentosa* is at the end of the panchloroin line, and *Polyphaga saussurei* has the same projection on the third axis as the Blattidae (with which I associate it phenetically). This last relationship is more noticeable in the large nymph males (Fig. 43), where *P. saussurei* lies between *C. punctulatus* and the Blattidae, presumably because the male of *P. saussurei* is considerably smaller and more slender than the female. One may speculate on the nature of the morphological specializations which place these three OTU's in proximity, for presumably they are not cladistically closely related. The details of their biologies are mostly unknown. *G. portentosa* is massive and apterous, as is the female of *Polyphaga saussurei.* The latter species is found in loess dust and in the burrows of rodents and desert turtles, according to Vlasov and Miram (quoted in Roth and Willis, 1960: 29). The same authors also describe the "swimming" through sand of the nymphs, alate males and wingless females of *Polyphaga indica* Walker. Fausek (quoted in Roth and Willis, 1960:29) reports similar behavior for *Polyphaga aegyptiaca* (L.). *Panesthia australis,* a dark, winged cockroach, is described as occurring in burrows under the thick bark of fallen and rotting trees (Shaw quoted in Roth and Willis, 1960:58) and in loose detritus (Tepper quoted in Roth and Willis, 1960:58). These heavy-bodied insects appear to be adapted to a "digging-burrowing" existence, and their phenetic similarities are the result of convergent evolution.

In Figures 38 and 41, the correlation phenograms, *Cryptocercus punctulatus* clusters with *Panesthia australis* before clustering with the blattids. According to McKittrick, *C. punctulatus* is related to the blattids. *C. punctulatus* and the blattids are even less close in the male distance phenogram (Fig. 42) where *C. punctulatus* again first joins with *P. australis*. *C. punctulatus* and *P. australis* actually pair in the correlation phenograms. Although they are near each other they are not mutually closest in the models (Figs. 40, 43). In fact, *C. punctulatus* in the models is closest to the panchloroins. Earlier classifications by numerous authors (cited by McKittrick, 1965) did indeed regard *C. punctulatus* and *P. australis* as related and placed them both among the blaberids. McKittrick's revision shifted *C. punctulatus* to what I believe is its correct position, near the blattids. In the large nymph males (Fig. 43), *C. punctulatus* and the blattids do have a common projection on the third axis. *C. punctulatus* and *Panesthia australis* are the only xylophagous cockroaches, which is the probable explanation for their convergence and isolation from their respective groups.

The Blattellidae form distinct clusters in both the models (Figs. 40, 43) and correlation phenograms (Figs. 38, 41). *Parcoblatta pensylvanica* lies in the gap between the other blattellids and the Blattidae in the models, and clusters with the panchloroins in both distance phenograms (Figs. 39, 42). Its adherence to another cluster in the distance phenograms may be understood by consulting the models. *P. pensylvanica* is much larger and thus has a higher first axis projection than the other blattellids. But it is also level with *Panchlora nivea,* a smaller OTU. Apparently, in the models there is, *within* families, a sorting according to size which is at least partially independent of the sizes of OTU's belonging to different clusters.

The gap between the two plectopterines is wider in the male than in the female models (Figs. 40, 43). *Lophoblatta fissa* is so remote from the other blattellids that in Figure 42 (males) it is the last to join the phenogram. This phenetic separation agrees with McKittrick's phyletic conclusions.

The Blattidae are a nicely discrete group in both models (Figs. 40, 43), but in the males (Fig. 43) *C. punctulatus* and *Polyphaga saussurei* are nearby and perhaps could be included. In the correlation phenograms (Figs. 38, 41), the family is divided into two separated clusters, which unite into a single cluster in the distance phenograms (Figs. 39, 42). The large nymph male cluster *L. albipalpus - Platyzosteria melanaria* in Figures 41 and 42 consists of very dark, apterous or brachypterous Blattidae which McKittrick assigns to three different subfamilies.

The phenograms do not divide the Polyzosteriinae from the Blattinae. McKittrick (1964:20-21) admits that this separation is difficult and that others may disagree with her placement of *Eurycotis*. She had considered *E. floridana* a blattine on the basis of behavior and proventricular structure, but her study of *Eurycotis pluto* Hebard led her to conclude that it had polyzosteriine genitalia and was in fact an anomalous member of this subfamily. This anomaly is reflected by the positions of *E. floridana* and *Platyzosteria melanaria* at the periphery of the blattid constellation in the models. The *Periplaneta* OTU's do not form a single cluster in the phenograms. *Periplaneta americana* clusters with *E. floridana* in Figures 41 and 42, and with *B. orientalis* in Figures 38 and 39.

6.2.3. Adults: Before entering into a discussion of individual families it is ap-

propriate to comment on the apparent association of the third axis with shape. The adult females of *Byrsotria fumigata, G. portentosa, H. litomorpha, Panesthia australis, C. punctulatus, Polyphaga saussurei* and *Attaphila fungicola,* OTU's of various families are all heavy-bodied, often brachypterous or apterous, and these are all high on the third axis (Fig. 46). More slender and usually alate OTU's have much lower third axis projections. Thus these traits (of shape) can be tentatively identified with the third factor in the models. It is interesting to note that the polarity is reversed in the males (Fig. 49). One exception is male *G. portentosa* which has a considerably higher third axis projection than would be expected from its appearance.

The Blaberidae are in the majority in the present study and encompass a wider range of morphological variation than any other family of cockroaches. This fact is illustrated by their elongate, band-like and almost linear distribution in the models (Figs. 46, 49). The blaberoins are situated at one end of this narrow band and the panchloroins at the other although there is some overlapping. In Figure 46, the adult female panchloroins *N. cinerea, L. maderae, C. patula* and *G. portentosa* are displaced from the other panchloroins (*D. punctata, Panchlora nivea* and the Pycnosceli) on one or more axes. In the males (Fig. 49), all of the panchloroins are more widely spread on axis I. *Panesthia australis* is considerably removed from the other blaberoins in the males but not in the females. The linear arrangement of the Blaberidae is obscured in the phenograms (Figs. 44, 45, 47, 48) where the family fragments into a number of clusters. None of the phenograms adequately expresses McKittrick's view of the Blaberoidea as comprising the Blaberidae, Blattellidae and Polyphagidae. But the models show that this view is reasonable from a phenetic standpoint.

Both *Phortioeca phoraspoides* (Zetoborinae) and *Panesthia australis* (Panesthiinae) are much smaller than the blaberines and consequently do not cluster with them in the phenograms and are removed from them in the models. McKittrick (1964:34) is of the opinion that the Zetoborinae and Panesthiinae are quite dissimilar but are linked by the blaberines to form the blaberoin complex. In the models *Phortioeca phoraspoides* and *Panesthia australis* are not too far apart.

The two epilamproin OTU's *Hyporhicnoda litomorpha* and *Audreia bromeliadarum* lie near the panchloroins (Figs. 46, 49). These OTU's are not mutually closest to each other in either the phenograms or the models (Figs. 44-49). In the studies of female genital and proventricular characters (Figs. 22-27), they cluster together only in the correlation phenograms. They do not cluster together in the phenograms based on male genital characters (Huber, unpubl.).

Of the panchloroins, the Oxyhaloinae, which are represented by three OTU's of very different sizes and shapes, are widely separated in all models and phenograms. *L. maderae* always joins the blaberoins and *N. cinerea* the panchloroins. The adult female of *G. portentosa* joins a mixed group of large heavy-bodied OTU's. The extremely isolated male clusters with Blattidae. This dispersion is in contrast to the behavior of the oxyhaloines when only genital characters are considered (Figs. 22, 23, and Huber, unpubl.).

The remaining panchloroins form moderately compact clusters in the models and phenograms. The panchlorines *Panchlora nivea* and *Capucina patula* are separated by other panchloroins in the models and do not cluster in the phenograms. They cluster together when female genital characters alone are employed

(Figs. 22, 23) but not when male genital characters are used (Huber, unpubl.). The models (Figs. 46, 49) show *C. patula* close to the oxyhaloine *N. cinerea*. The proximity between these two OTU's, however, may be due to similarity in size. When judged on genital characters, *Capucina* shows little affinity with the Oxyhaloinae (McKittrick). The present study of female genital characters confirms this view but analysis of proventricular characters does not.

Interesting morphological specializations in two panchloroin OTU's do not seem to have affected their phenetic placement. Adult *Panchlora nivea* are green rather than some shade of brown. *D. punctata* has an unusual method of wing-folding and aberrant venation. In fact, Rehn (1951) weights these features so heavily that he erects a monogeneric family to accommodate *Diploptera*.

The Blattellidae form compact groups in the models and phenograms except for the adult female of *Attaphila fungicola*. This OTU joins *Arenivaga erratica*. Then both join the major blattellid cluster *B. germanica* - *S. longipalpa* in the correlation phenogram (Fig. 44) but are the last to join the other OTU's in the distance phenogram (Fig. 45). The female genitalia of *Attaphila fungicola* are characterized by the following: (a) crosspieces are present, (b) the brood sac is absent, (c) valvifers I-a are present and fused anteriorly, thus forming the support for the membranous roof of the genital chamber, (d) the spermathecal plate is single and anterior, lying against the anterior end of valvifers I-a, (e) the basivalvulae are absent and (f) valves I do not laterally embrace valves II and III. By McKittrick's criteria, on the basis of *a* above, this species belongs to the Blaberoidea and *b* and *c* place it in the Blattellidae rather than in the Polyphagidae or Blaberidae. Allocation to subfamily is more difficult. It does not belong to the Anaplectinae, Ectobiinae or Nyctiborinae, all of which have distinctive genitalia. The remaining characters, with one exception, are not sufficient to assign membership in either the Plectopterinae or Blattellinae. Only *f* indicates a plectopterine affiliation. Clustering of OTU's using only female genital characters (Huber, unpubl.) shows *A. fungicola* joining with the blaberids *A. bromeliadarum* and *H. litomorpha*, but this may be due to the absence of information regarding the seven characters of the spermatheca and genital papilla (cf. Ehrlich and Ehrlich, 1967, discussing the relationship of the skippers to the butterflies).

In the adult female correlation and distance matrices of both sexes, *A. erratica* ranks closest in column *A. fungicola* followed by the blattellids. *Attaphila fungacola* is a minute cockroach but except for size bears a remarkable resemblance to *Arenivaga erratica*. Both are oval, apterous and setose. This similarity is not presently separable into patristic and homoplastic components (as defined by Sokal and Camin, 1965). It is not surprising that the two were placed in one superfamily by Princis (1960). It is probably this similarity in shape which projects *A. fungicola* higher on the third axis than the other blattellids. Further, *A. fungicola* has the same second axis projection as the rest of the blattellids and could be placed among them if we ignore size (axis I). Therefore, I would second McKittrick's (cited in Roth, 1968b) removal of *A. fungicola* from the Polyphagoidea to the Blattellidae and would like to suggest that the status of the Atticolidae be likewise re-examined. This family is also associated with ants (for references, see Roth and Willis, 1960) and also placed in the Polyphagoidea by Princis (1960).

Most of the remaining Blattellidae cluster together in the distance phenograms

(Figs. 45, 48) and show a division into plectopterine and blattelline subclusters in the correlation phenograms (Figs. 44, 47). The exception is the adult female *I. deropeltiformis* which joins another cluster in Figure 44 and is also isolated in the distance phenogram (Fig. 45) and in the model (Fig. 46). The most obvious difference of *I. deropeltiformis* from other blattellines is in its large number of spermathecae, but this character was not employed in the factor analysis. Presumably then, there are other more subtle, undiscovered differences. The male seems unexceptional and its position in the model (Fig. 49) substantiates this impression. *Xestoblatta festae* (Griffini), studied by McKittrick (1964), also has a large number of spermathecae. Inspection of correlation and distance phenograms (employing all of McKittrick's OTU's computed from her Tables 4 and 5 [Huber, unpubl.]) shows that *X. festae* is also an isolated blattelline. Because of the limited sampling of blattelline genera by both McKittrick and myself it is not possible to evaluate the significance of this isolation.

The separation into blattellid subfamilies is not apparent in the models (Figs. 46, 49). *S. longipalpa* clusters with the Blattellinae, and *L. fissa* is isolated in both models, but by a greater distance in the male. In studies of male (Huber, unpubl.) and female (Fig. 13) genital characters the correlation phenograms show the Blattellinae and Plectopterinae in separate subclusters.

The relationships of the polyphagids differ considerably between the sexes. In the adult males, *A. erratica* and *Polyphaga saussurei* cluster together and then join a large cluster composed of blattellids and panchloroins (Fig. 47). In the model (Fig. 49), the adult male of *P. saussurei* lies between the Blattidae and Blaberidae while *A. erratica* is within the panchloroin group. In the females, *A. erratica* and *A. fungicola* join and cluster with blattellids while *P. saussurei* unites with *G. portentosa* (Fig. 44). Much of the difference between adult female *A. erratica* and *P. saussurei* in Figure 46 is along the first and third axes. This substantiates my impression that the main difference between these OTU's is associated with size.

It is tempting to speculate that additional species of adult female Polyphaginae of an intermediate size would be located within a hyperellipsoid (in Fig. 46) with these two OTU's at the ends of the major axis. (The affinities of *C. punctulatus* may become clearer if this were done, for although it is not too near either polyphagid it would be quite close to the surface of this hyperellipsoid.)

In the correlation phenogram computed from female genital characters (Huber, unpubl.), *A. erratica* and *Polyphaga saussurei* unite and are joined by *C. punctulatus*. This cluster then fuses with one containing all the Blattidae. This lends support to McKittrick's view that there are many general similarities between the families Cryptocercidae and Polyphagidae. She adds that the nature of the similarities indicates that both families represent primitive stocks, and indeed both are centrally located in the phenetic hyperspace delimited by this model (Fig. 46). But in the adult male model (Fig. 49), the polyphagids are not close to *C. punctulatus*. A study of male genital characters (Huber, unpubl.) shows the polyphagids clustering with the Blattidae. To summarize—adult male Polyphagidae studied by me resemble the blattoids in genital characters and the blaberoids in nongenital ones. It is very probable that the Polyphagidae resemble the basal stock of both blattoids and blaberoids.

Cryptocercus punctulatus and *Panesthia australis* cluster in all adult phenograms

and are close to each other in both models (Figs. 44-49). The models clarify their relationship, showing that both are aberrant members of the groups to which they are assigned (*C. punctulatus* to the Blattoidea and *P. australis* to the Blaberidae), and that the kind of morphological specialization they exhibit causes them to converge. McKittrick's system is reflected in the rankings of these two OTU's in the adult female distance matrix: in column *C. punctulatus, B. orientalis* ranks closest and *P. australis* fourth, while in column *P. australis, G. portentosa* and *C. punctulatus* are ranked highest.

In the studies of male genital characters (Huber, unpubl.), the adult male *C. punctulatus* shows interesting relationships. In the correlation phenogram it clusters, as one would expect, with *L. albipalpus*. In the matrices the rankings are as follows:

Correlation Coefficient

Rank	OTU	*r*
1.	*C. punctulatus*	1.000
2.	*P. saussurei*	0.252
3.	*B. vaga*	0.141
4.	*B. germanica*	0.129
5.	*L. albipalpus*	0.126
6.	*E. floridana*	0.088
7.	*S. longipalpa*	0.040
8.	*P. australis*	0.034

Distance Coefficient

Rank	OTU	*d*
1.	*C. punctulatus*	0.000
2.	*P. australis*	1.342
3.	*B. vaga*	1.432
4.	*D. punctata*	1.509
5.	*B. germanica*	1.532
6.	*A. bromeliadarum*	1.544
7.	*H. litomorpha*	1.573
8.	*P. saussurei*	1.586

Its proximity to *Polyphaga saussurei* and relative distance from the nearest blattid should be noted in the correlation coefficients. The ranking of *P. australis* in the distance column is more surprising for it implies that even in genital characters *Panesthia australis* shows relatively high phenetic similarity to *C. punctulatus*. On the basis of male genitalia, *C. punctulatus* shows close similarities to members of all the other families. In both adult models, the closest blattid in column *C. punctulatus* is the primitive *L. albipalpus*. These are yet other indications of the generalized nature and central position of *C. punctulatus* among the Blattaria.

The blattid subfamilies are clearly defined. All the Blattidae form a single cluster in the female (Figs. 44, 45) but not in the male (Figs. 47, 48) phenograms. In the female phenograms, *B. orientalis* first clusters with *L. albipalpus* and the polyzosteriines, all of which are brachypterous. In the female model (Fig. 46), *B. orientalis* is slightly higher on the third axis than its blattine relatives, the macropterous Periplanetae, bringing it closer to *L. albipalpus* and the polyzosteriines. This may be due to differences in wing length between the two groups. In the male phenograms, *L. albipalpus* and the polyzosteriines also cluster together, but *B. orientalis* joins the other Blattinae. The male *B. orientalis* does have longer wings than the female. The Lamproblattinae and Polyzosteriinae have the lowest and highest third axis projections of the blattids in the male and female models, respectively. This accords well with the identification of the third factor in the adults.

Periplaneta americana clusters with *B. orientalis* in male phenograms (Figs. 47, 48) before joining the other Periplanetae. The *Periplaneta* OTU's are together in the female phenograms, but *P. americana* is the last to join. In the clustering of OTU's using female genital characters only (Huber, unpubl.), *P. americana* is added only after *B. orientalis* and the

other *Periplaneta* OTU's have coalesced. A study of male genital characters (Huber, unpubl.) reveals that *P. americana* is the last member of its genus to join the *Periplaneta* cluster. Thus, in both sexes of all stages studied and for no obvious reason, *P. americana* is consistently isolated from its congeners.

6.3. Changes in classification along the ontogenetic axis

It is only when the OTU's are examined as an ontogenetic series that a shifting pattern of family relationships emerges. An examination of Figures 34, 40 and 46 (females) and 37, 43 and 49 (males) reveals a gradual separation of the OTU's into family constellations during ontogeny. Individual OTU's that are with their families as small nymphs are often dispersed and separated as large nymphs. This can be explained by regarding each OTU as either an advance or vanguard member of a family migration taking place in the space encompassed by the model (representing changes in morphology) and in time (representing changes in ontogeny). By the time these stray OTU's have become adults many of them have rejoined their family group. Much of the movement of families appears as a shifting along axis II. This tempts one to speculate that this axis is at least partly correlated with morphological changes during maturation.

6.3.1. Females: Many of the small nymph OTU's (Fig. 34) form a mixed loose constellation of several families including some blattids and most of the panchloroin complex of the Blaberidae. The constellation holds together in all three dimensions, reflecting the lesser differentiation and greater similarity of its members to each other. By adulthood (Fig. 46) these OTU's have drifted apart and in most cases have come to lie with their own families.

The Blaberidae are mostly scattered in a band along axis I. Even in the small nymphs there is a good separation between the blaberoins on the positive and the panchloroins on the negative portions of axis I, though there is some overlapping. This separation is maintained into adulthood. As small nymphs, the blaberids form an elongate band mostly on the negative side of axis II. As large nymphs they are arranged on both sides of this axis, the blaberoins being more scattered. By the time they have become adults they again form an elongate band but this time on the positive side of axis II. The position of the OTU's in different stages suggests a migration over a period of time. This is a good example of a family which appears more scattered at a later stage (large nymphs) because of different rates of migration of individual members.

The small nymph female blattellids form a compact constellation except for *Parcoblatta pensylvanica*. As large nymphs, they appear to be somewhat more scattered. As adults, they coalesce into a compact group around *Parcoblatta pensylvanica,* which has more or less maintained its position through all stages. The blattids are partly scattered among the mixed constellation as small nymphs. They are already a well-defined family as large nymphs and well separated in all three dimensions. As adults they have become quite isolated from the other OTU's.

Small nymph *Cryptocercus punctulatus* is part of the mixed constellation. This OTU does not move far from its original position throughout ontogeny at least in the first and second dimensions. As a large nymph, *C. punctulatus* lies among the remnants of the mixed cluster (mostly panchloroins) which have not yet migrated to their adult positions. The adult *C. punctulatus* is well separated along the third axis from the other surrounding OTU's (now blattellids). On this axis it

is level with the blattids with which it is usually classified in the superfamily Blattoidea.

Polyphaga saussurei lies on the outskirts of the mixed cluster as a small nymph but even here it is somewhat separated by its height on the third axis. Although it moves up on the first axis, as a large nymph it is level with many of the blattids on axis III and remains fairly near them as an adult. It is interesting to note that *P. saussurei* takes up a position midway between the blattoids and blaberoids as an adult, since it has phenetic similarities with both superfamilies. This has been discussed previously.

6.3.2. Males: In general the same migration and coalescence of families is also found in the males (Figs. 37, 43 and 49). The mixed constellation is again present in the small nymphs although its members are more separated into family groups than they were in the females.

The band-like formation of the blaberids is not clearly apparent until adulthood and cuts diagonally across all axes. The panchloroins and blaberoins come to be reasonably well separated with a few exceptions, as before. Both blattellids and blattids become increasingly isolated as families, but the blattids come to lie on the opposite side of axis II from their position in the females. The compactness of a family as adults, especially in the case of the Blattidae and Blattellidae, must be in part due to the development of the characteristic genitalia. This phenomenon is masked in the case of Blaberidae by the great variation in size among the OTU's (scatter along axis I).

In the males, *Cryptocercus punctulatus* shifts to the negative side of axis II and to the positive side of axis I during ontogeny. This is in contrast to its behavior in the females where it remains in more or less the same position throughout. There is no obvious reason for this sex difference other than development of the genitalia. These, of course, are not present until the adult. Yet *C. punctulatus* has shifted its position even as a large nymph. However, it should be noted that because the position of a particular OTU is relative to all other OTU's it is possible that a shift may be due to morphological changes in all others rather than (or, as well as,) in the one being considered.

Polyphaga saussurei (not available as a small nymph male) moves along as a distant satellite of the blattids much as it does in the females.

7. DISCUSSION AND CONCLUSIONS

7.1. General remarks

The classifications of the Blattaria presented in this study (Figs. 28-49) resemble those of McKittrick in most respects. The two general classifications (Figs. 28-31) both show many similarities to classifications of individual stages and sexes (Figs. 32-49), but the one based on adult characters only agrees best with that of McKittrick.

According to von Baer (from De Beer, 1958), during ontogeny general characters appear before special characters. He also states that animals show progressive divergence in form from each other during their development. These generalizations are well illustrated by my studies of the various instars for, while families are ill-defined in the small nymph models, the family clusters become increasingly distinct in the large nymphs and adults.

However, in the ontogenetic sequences discussed in Section 6.3, there are a few small nymph OTU's which are closer to their group than are the large nymphs or adults (e.g., male *Lophoblatta fissa*), as well as the opposite case where adult OTU's are closer to their group than are large or small nymphs (e.g., female *Parcoblatta pensylvanica*). These OTU's are

examples of ontogenetic divergence from, or convergence with, the statistical type of a group (Sokal, 1962). The statistical type represents the morphological norm and is situated at the centroid of a cluster in hyperspace (though there is not necessarily an OTU at those coordinates). Changes over a period of time in the position of OTU's relative to the group type may perhaps be regarded as ontogenetic and purely phenetic analogs of the morphological modes of evolution summarized by De Beer (1958:36-37). For example, maximum displacement from the group in a small nymph is analogous to either caenogenesis or acceleration and maximum divergence as an adult to either neoteny or adult variation. In the models, distance between OTU's is a measure of their phenetic morphological difference. An OTU that is consistently far from its group, or that changes its relative position with time, is one that deserves further investigation. It may well prove to be distinctive in areas other than its morphology.

7.2. Use of the term "classification"

A classification is a system by which taxa are ranked in a hierarchical fashion (Simpson, 1961; Sokal and Sneath, 1963; Hennig, 1965). I would like to expand this classical concept to include schemes of classification which employ phenograms, cladograms, phylograms and models of various dimensions. Phenograms are similar to hierarchic arrangements in that both are systems of nested categories, but phenograms have the additional advantage of permitting one to place the classification on a quantitative basis. Models, which at first sight do not appear to be classifications, may be transformed into phenograms by calculating the taxonomic distances between all pairs of OTU's and then submitting this matrix of distances to cluster analysis. Indeed, if the constellations in a model could somehow be suitably joined, they would appear to be arranged in a hierarchic manner.

7.3. Models as 3-dimensional classifications

Information about the relationships of OTU's in a taxon to OTU's of another taxon is lost in phenograms and other hierarchic arrangements. This difficulty can be overcome by the use of models where the distance between any two OTU's may be seen and calculated from their coordinates. Such models are used by Boyce (1964) in studies of hominoids, Rohlf in work on mosquitoes (1967) and bees (1968), and Moss (1967) on mesostigmatid mites. Du Praw (1964, 1965) has produced two-dimensional models in which the axes are discriminant coefficients derived from measurements of worker honeybee wings. He is so enthusiastic about his methods that he proposes these techniques for adoption as the basis of a completely quantitative non-Linnean taxonomy.

In my six data sets, the sums of squared factor loadings (equivalent to the eigenvalues resulting from a principal component analysis) of the first three factors are quite low. Reification of the factors has not been entirely possible. As in other studies of this type, Factor I represents the general size of the organism. The movement of OTU's during ontogeny suggests the possibility that Factor II is concerned with the morphological changes that accompany maturation (Section 6.3). In the adult models at least, Factor III seems to be identified with "body shape": slender, elongate, macropterous versus heavy, rounded, brachypterous or apterous (Section 6.2.3). The r_{coph} values between the models and their similarity matrices are no higher than those between the phenograms and theirs (Tables 6-11). Nevertheless, models are a useful visual tool in the analysis of my data, for patterns of

clustering difficult to understand in the phenograms become instantly comprehensible. If the clusters of OTU's in the phenetic hyperspace are hyperspheroids separated by distinct gaps, then both models and phenograms should produce equally clear-cut classifications. But once the models based on my data were constructed, it became clear that the clusters representing the families and complexes formed constellations which are often close to each other or actually interdigitating. Rohlf (1967), employing the same methods, finds his elongated clusters close to one another but without overlapping. Like him, I note that the OTU's misplaced in the phenograms are those which are at the periphery of a constellation or displaced laterally from it. Rohlf (1967) suggests that phenograms could be improved by a method of cluster analysis where at each step, the shape of each cluster is evaluated. This produces information which modifies the rules for addition of subsequent OTU's. He believes that such a method would reassign poorly placed OTU's to a better position in the phenogram.

Rohlf's comment (1967) that elongation of a cluster implies a high degree of correlation among characters within the cluster is particularly interesting. This appears to be related to my observation (Section 6.2.2) that there is a sorting of OTU's by size, within clusters, which is partially independent of sorting by size in other clusters. It is as if the phenetic hyperspace between clusters has become warped so that OTU's of equivalent size but in different clusters do not have the same projection on the first axis. Of course, the differences are due to the fact that additional characters influence the projection of an OTU on the first axis. Blackith and Albrecht (1959:15-16) state "that we are trying to see how alike are groups of insects in respect of all characters measured, [and] it is noteworthy that Einstein (1950:81) has remarked 'the coordinates, by themselves, no longer express metric relations, but only the "neighborliness" of the things described'."

7.4. Comparison between the classifications of the present study and those of McKittrick

The classifications constructed in this study agree in most respects with those of McKittrick, despite the fact that we used different sets of characters. The differences do appear to be a consequence of the kinds of characters employed. Models and phenograms (Figs. 1-27) based on McKittrick's data show large gaps between families and subfamilies. These result from her use of character suites chosen to emphasize differences between OTU's with the aim of elucidating the phylogeny of cockroaches. My study, because it is intended to be phenetic, utilizes much larger numbers of characters. The sole criterion employed in selecting a character was that it not be invariant. Although an exhaustive number of characters was not used, no conscious a priori selection was made. The interdigitation or close contact between the families of my study is due, I believe, to the use of characters which exhibit common character states in many of the OTU's (Table 3; Section 7.5). One objective of the study is the comparison of nymphal and adult classifications. Many characters used in adult classifications (wing and genital) are, of course, not present in nymphs. Despite this, there is good agreement between my nymphal classifications and those of McKittrick (adults only). This independently confirms her groupings of the Blattaria and also shows that nymphal characters exist which can be exploited in blattarian taxonomy.

In many of my models, the groupings of families and complexes are very similar to those in McKittrick's phylograms. In

fact it is possible to convert the former into the latter merely by drawing arrows to indicate phyletic trends. Colless (1967a) states that in entomology at least, classifications are essentially phenetic because of the paucity of fossil material. Yet McKittrick has managed to use phenetic characters to derive a plausible phylogenetic scheme of relationships for her taxa. Gould (1967) also constructs a satisfactory phylogeny when he applies factor analysis to phenetic data of the pelycosaurs. Colless (1967b), commenting on the cladogram of cytochrome *c* produced by Fitch and Margoliash (1967), notes that their method of analysis is essentially a phenetic one. McKittrick's data (1964, her Tables 1-7) would be excellent material for testing and refining methods of constructing cladograms, such as those developed by Camin and Sokal (1965), Fitch and Margoliash (1967), Cavalli-Sforza and Edwards (1967), Inger (1967), Horne (1967), Throckmorton (1965), Wilson (1965) and Zuckerkandl (1965).

7.5. *Significance of factor loadings and the hypothesis of the factor asymptote*

Many characters chosen for this study were virtually invariant, i.e., the majority of OTU's were in the same state (Section 2.2). Such characters contribute very little information to the classification, but there are valid reasons for not discarding them. Mayr (1965) explains that the orthodox taxonomist ignores characters with low information content, i.e., those with low loadings on all factors. This is a perfectly acceptable procedure but, in this study, would have left no characters of known value in the nymphs. Because of this and so that comparisons could be made between adults and nymphs using the same characters, it was legitimate to retain them. The use of many characters in this fashion is useful for the production of special classifications. Sokal and Sneath (1963) recommend the use of such large numbers because it is impossible to predict the value of a character to a classification. One of the dividends of classifying by factor analysis is that an a posteriori weight is assigned to each character. This is a signal advantage of this method over cluster analysis. If greater separation between clusters is deemed desirable, then characters with low loadings on all factors may be eliminated from future analyses. Diagnostic keys may be prepared from such data (Sokal and Sneath, 1963: 319) and discriminant analyses (Fisher, 1936) can also be performed where identification is difficult, for instance, in immature forms.

Use of large numbers of characters provides useful insight into certain theoretical problems of numerical taxonomy. Blackwelder (1964) fears that if all possible characters are used, the significant ones would be overwhelmed. I do not think this is happening here because, as Rohlf (pers. comm.) points out, if the characters are random in their distribution, then they will not have any effect on the classification. Rather, I believe that the proximity of the clusters in my classifications is an indication that Sokal and Sneath's (1963) factor asymptote (for external exoskeletal characters at least) has been surpassed. The factor asymptote hypothesis states that in a given study, after a certain number is reached, addition of more characters contributes very little new information and is therefore unprofitable. This asymptote has obviously not been reached in McKittrick's data with their very discrete groupings.

A surplus of characters includes not only data for taxonomic separation but also much that is part of the common genetic heritage of all cockroaches. The kind of character included in the common genetic heritage is the one with a low information content referred to at

the beginning of this Section. Characters such as color, setal counts and measurements fall into this category. Du Praw (1964) reached a level where, after three cycles of classification of his worker honeybees, no new groups appeared. According to him, at this point taxonomic classification merges with the analysis of morphogenetic growth patterns as carried out by Blackith (1960). Du Praw is no doubt tapping the common genetic heritage of his material at this level.

7.6. Incongruence of classifications, mosaic evolution and the nonspecificity hypothesis

My data show at least fair congruence among classifications of all stages and sexes (Section 6.1). This proves that it is possible to classify even very young stages of Blattaria to some degree. Furthermore, the r_{coph} values between matrices are the same no matter which coefficient of similarity is used. This is in contrast to Rohlf (1963) who notes that the cophenetic correlation between larval and adult mosquitoes using distances is much higher (0.591) than one based on correlations (0.293). The reason for this discrepancy is not clear. Since size differences are so important in my study, I would have expected the correlations, which are less affected by size than the distances (Boyce, 1964), to show greater congruence between classifications. Since they do not, classifications based on distances are judged equally useful.

When many characters are used, we are dealing with the effects of many genes. Most genes are pleiotropic and, according to Sokal and Sneath's (1963) nonspecificity hypothesis, manifest their action in many different parts of the body. If this is so, then one body area should produce as good a taxonomic analysis as another since its characters will represent a similar and adequate sampling of the genome. Of course, classifications from different body regions are not always congruent. For instance, there are differences in McKittrick's classifications based on proventricular and genital characters (Sections 4.2-4.7). Likewise, Ehrlich and Ehrlich (1967), Moss (1968) and Michener and Sokal (1966) find only weak support for the nonspecificity hypothesis in their data. The nonspecificity hypothesis is also not tenable when mosaic evolution has occurred, so these conclusions are not surprising. Sneath (1964) comments on the problem of incongruence of classifications and mosaic evolution while Emden (1957) discusses the different degrees of incongruence to be found in classifications of larval and adult insects. De Beer (1958) also discusses incongruence but from the standpoint of heterochrony of gene action.

7.7. Selecting a general classification

Ideally, it would be desirable to create a single general classification for any particular group. This could then be used as a reference for all other classifications of that taxon. But as Sneath (1961) points out, even a phyletic classification is a special one, and Ehrlich (1964) states that all classifications are biased to some extent. Nevertheless, Rohlf (1963) believes that a general classification can be produced and makes suggestions for adequate sampling of characters from different organ-systems and life-history stages. However, it seems to me that such a classification based on overall similarity would result in a loss of information when mosaic evolution is involved. A good example of this is the case of *Eurycotis floridana* which is, according to McKittrick, polyzosteriine in genital and blattine in proventricular characters. In both of my general classifications (Section 5), it clusters with *Platyzosteria melanaria* (Polyzosteriinae). Both are separate from the Blattinae. McKittrick's decision to

place *E. floridana* in the Polyzosteriinae appears justified but it is a compromise. Because of its blattine characteristics, its true position would be better illustrated by a series of special classifications. This is the view of Ehrlich and Ehrlich (1967). These authors point out that there is no "correct" set of phenetic or phylogenetic relationships, and that the taxonomist merely uses as a standard the one with which he is most familiar.

7.8. A standard classification based on a comparison of genomes

It may be possible to base a standard classification on a comparison of genomes. This arises from the idea that when the characters of the phenome, or phenotypic analog of the genome (Soulé, 1964), are sampled, we are actually attempting to sample the genome. This subject is interestingly discussed by Ehrlich (1964), who concludes that a general taxonomy based on genomes is probably unattainable. Mayr (1965) and Johnston (1964) also discuss the relationship of genotype to phenotype. Throckmorton (1965) in particular raises a problem which bears on the present study. In discussing genotypic homology, he is concerned with a character which may appear independently in several descendant forms derived from a species which lacked the character in question. He postulates that the potential for the character lay "unassembled" in the gene pool of the ancestral species. For example, if the wingless condition of some cockroaches is due to neoteny, it may be that the genes necessary to produce the wings are still present in the genome. In that case, comparison of the genomes of winged and apterous species might show them to be similar. However, it is probably impossible to weight or correct for the fact that the genes under consideration are active in one species and inactive in the other.

7.9. Neoteny in Orthoptera and its bearing on classification

Neoteny appears to be a widespread condition in the Orthoptera. The occurrence of supplementary reproductives in termites (Gay, 1955) and the *solitaria* phase of the migratory locust (Kennedy, 1956) are regarded as examples in nature. Wigglesworth (1954) mentions studies with various apparently neotenous Orthoptera (crickets, cockroaches and stick insects). Bodenstein (1953) finds that if adult female *Periplaneta americana* are made to molt, a larger adult is produced where the seventh sternum differentiates beyond the normal adult condition. Wigglesworth (1965) reports on Pflugfelder's production of giant adults of the phasmid *Carausius*. These show partial development of a median dorsal ocellus, an adult character not normal in this species.

Girardie (1961) has made a biometrical study of "giant adults" in *Periplaneta americana*. It would be interesting to produce such individuals in wingless or brachypterous species to see if wings are actually formed. It should then be profitable to compare these by morphometric methods with normal adults and with adults of related winged species.

7.10. Future prospects

Many additional investigations are possible using these collected data. One of these is a study of the degree of sexual differentiation of these species at each stage. A comparison with the elegant work of Blackith (summarized, 1965) on the Orthoptera, Hemiptera and Hymenoptera should be most interesting. A detailed quantitative study of the ontogenetic analogs of De Beer's morphological modes of evolution (see Section 7.1) should also be possible. Hurlbutt (1964, 1968) attempts to relate the degree of similarity between species of two genera of mesostigmatid mites to the frequency

with which they are found together. He concludes that species which are moderately similar to each other are found together more often than either very similar or markedly dissimilar species. Examination of my data could reveal suitable species for similar experimental analysis of interspecific competition, for example, between species of *Periplaneta* or between the early instars of *Parcoblatta pensylvanica* and *Periplaneta americana* (Figs. 34, 37).

Finally, numerical taxonomic analyses may aid in the integration of Recent and fossil classifications of Blattaria. Only the classifications of Karny (1921) and Bey-Bienko (1950) have attempted this. Multivariate analysis should be of value in clarifying the relationships within this huge assemblage of forms, probably by comparison between the wings of Recent and fossil specimens, since that is usually the only part preserved.

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TABLE 1. The species of cockroaches studied, their allocation to family and subfamily in McKittrick's classification and the sources of the specimens.

Species	Family and Subfamily	Source
Archimandrita tessellata Rehn	Blaberidae, Blaberinae	Harvard Univ.
Arenivaga erratica (Rehn)[a]	Polyphagidae, Polyphaginae	Dr. D Elden Beck
Attaphila fungicola Wheeler	Blattellidae, ?Blattellinae	Dr. John C. Moser
Audreia bromeliadarum Caudell	Blaberidae, Epilamprinae	Harvard Univ.
Blaberus craniifer Burmeister[e]	Blaberidae, Blaberinae	Harvard Univ.; Kansas State Univ.; Virginia Polytechnic Inst.
Blaberus discoidalis Serville[e]	Blaberidae, Blaberinae	Harvard Univ.; Kansas State Univ.
Blaberus giganteus (Linnaeus)[e]	Blaberidae, Blaberinae	Harvard Univ.; Kansas State Univ.; Virginia Polytechnic Inst.
Blatta orientalis Linnaeus	Blattidae, Blattinae	Kansas State Univ.
Blattella germanica (Linnaeus)	Blattellidae, Blattellinae	Virginia Polytechnic Inst.
Blattella vaga Hebard	Blattellidae, Blattellinae	Virginia Polytechnic Inst.
Byrsotria fumigata (Guérin)[e]	Blaberidae, Blaberinae	Harvard Univ.; Dr. L. M. Roth
Capucina patula (Walker)	Blaberidae, Panchlorinae	Harvard Univ.
Cryptocercus punctulatus Scudder	Cryptocercidae, Cryptocercinae	Dr. L. R. Cleveland
Diploptera punctata (Eschscholtz)	Blaberidae, Diplopterinae	Harvard Univ.; Dr. L. M. Roth
Eublaberus posticus (Erichson)	Blaberidae, Blaberinae	Harvard Univ.
Eurycotis floridana (Walker)[e]	Blattidae, Polyzosteriinae	Harvard Univ.; Dr. L. M. Roth
Gromphadorhina portentosa (Schaum)	Blaberidae, Oxyhaloinae	Harvard Univ.; Dr. L. M. Roth
Hyporhicnoda litomorpha Hebard[a]	Blaberidae, Epilamprinae	Dr. L. M. Roth
Ischnoptera deropeltiformis (Brunner)[a]	Blattellidae, Blattellinae	collected at Lawrence, Kans.
Lamproblatta albipalpus Hebard	Blattidae, Lamproblattinae	Dr. F. A. McKittrick
Leucophaea maderae (Fabricius)	Blaberidae, Oxyhaloinae	Kansas State Univ.
Lophoblatta fissa (S. and Z.)	Blattellidae, Plectopterinae	Dr. F. A. McKittrick
Nauphoeta cinerea (Olivier)	Blaberidae, Oxyhaloinae	Kansas State Univ.
Panchlora nivea (Linnaeus)	Blaberidae, Panchlorinae	Harvard Univ.
Panesthia australis Brunner[e]	Blaberidae, Panesthiinae	Dr. M. J. Mackerras
Parcoblatta pensylvanica (De Geer)[e]	Blattellidae, Blattellinae	collected at Lawrence, Kans. and reared by author
Periplaneta americana (Linnaeus)[e]	Blattidae, Blattinae	collected at Lawrence, Kans. and reared by author
Periplaneta australasiae (Fabricius)[e]	Blattidae, Blattinae	Virginia Polytechnic Inst.
Periplaneta brunnea Burmeister[e]	Blattidae, Blattinae	Dr. C. A. Leone
Periplaneta fuliginosa (Serville)[e]	Blattidae, Blattinae	Virginia Polytechnic Inst.
Phortioeca phoraspoides (Walker)	Blaberidae, Zetoborinae	Harvard Univ.
Platyzosteria melanaria (Erichson)[e]	Blattidae, Polyzosteriinae	Dr. M. J. Mackerras
Polyphaga saussurei (Dohrn)[a]	Polyphagidae, Polyphaginae	Prof. G. Ya. Bey-Bienko
Pycnoscelus indicus (Fabricius)[b, e]	Blaberidae, Pycnoscelinae	Dr. L. M. Roth
Pycnoscelus surinamensis (Linnaeus)[c, e]	Blaberidae, Pycnoscelinae	Dr. L. M. Roth
Supella longipalpa (Fabricius)[d, e]	Blattellidae, Plectopterinae	Virginia Polytechnic Inst.; also collected at Lawrence, Kans. and reared by author
Symploce hospes (Perkins)	Blatellidae, Blattellinae	Dr. L. M. Roth

[a] Studied from dried specimens.
[b] This is the bisexual form of *P. surinamensis;* see Roth (1967a).
[c] Roth (1967a) restricts this name to the parthenogenetic form.
[d] The same as *Supella supellectilium* (Serville); see Princis (1963:249).
[e] Small nymphs were known to be first instar.

TABLE 2. Number of specimens per OTU. All OTU's for species not in the following list contain three specimens.

Species	Adult female	Adult male	Large nymph female	Large nymph male	Small nymph female	Small nymph male
Archimandrita tessellata	3	..	1	..	..	..
Arenivaga erratica	1	1	..	..	..	..
Attaphila fungicola	1	..	..	..	..	..
Audreia bromeliadarum	3	3	..	..	..	..
Capucina patula	3	3	..	..	..	..
Cryptocercus punctulatus	3	3	3	2	3	3
Eublaberus posticus	3	3	..	..	..	..
Gromphadorhina portentosa	3	3	1	3	3	3
Hyporhicnoda litomorpha	3	3	..	..	..	..
Ischnoptera deropeltiformis	1	3	..	..	..	..
Lamproblatta albipalpus	3	3	3	1	3	3
Leucophaea maderae	10	10	10	10	10	10
Panchlora nivea	3	3	3	1	3	3
Periplaneta americana	10	10	10	10	10	10
Phortioeca phoraspoides	3	3	..	..	..	..
Polyphaga saussurei	3	3	3	1	3	..
Pycnoscelus surinamensis	3	..	3	..	3	..
Symploce hospes	3	3	..	..	..	..

TABLE 3. Frequency of kinds of characters for each body region.

Body region	Kinds of characters					% of grand total
	Measurement	Color pattern	Setal count	Other	Total	
General	1	0	0	1	2	0.4
Head	28	18	0	3	49	11.0
Cervix	0	0	0	1	1	0.2
Thorax proper	4	44	0	22	70	15.6
Legs	9	9	34	8	60	13.6
Wings	7	11	0	44	62	13.9
Abdomen (excluding genitalia)	6	27	0	43	76	17.0
Female genitalia	0	0	0	50	50	11.2
Male genitalia	0	0	0	76	76	17.0
Total	55	109	34	248	446	
% of grand total	12.3	24.4	7.6	55.7		100

TABLE 4. Classification of Blattaria proposed by McKittrick. Only subfamilies and OTU's represented by material in the present study are included.

	Abbreviated name	Symbol on plan view of models
Suborder Blattaria		
Superfamily Blattoidea		
Family Cryptocercidae		
Subfamily Cryptocercinae		
Cryptocercus punctulatus	CRYPT	■
Family Blattidae		
Subfamily Lamproblattinae		
Lamproblatta albipalpus	LMPRB	○
Subfamily Blattinae		
Blatta orientalis	BLORN	○
Periplaneta americana	PERAM	○
Periplaneta australasiae	PERAS	○
Periplaneta brunnea	PERBN	○
Periplaneta fuliginosa	PERFL	○
Subfamily Polyzosteriinae		
Eurycotis floridana	EURYC	○
Platyzosteria melanaria	PLTYZ	○
Superfamily Blaberoidea		
Family Polyphagidae		
Subfamily Polyphaginae		
Arenivaga erratica	ARENV	□
Polyphaga saussurei	PLYPH	□
Family Blattellidae		
Incertae sedis		
Attaphila fungicola	ATPHL	▲
Subfamily Plectopterinae		
Lophoblatta fissa	LPHBL	▲
Supella longipalpa	SUPEL	▲
Subfamily Blattellinae		
Blattella germanica	BLGRM	▲
Blattella vaga	BLVAG	▲
Ischnoptera deropeltiformis	ISHNP	▲
Parcoblatta pensylvanica	PRCBL	▲
Symploce hospes	SMPLC	▲
Family Blaberidae		
Blaberoin Complex[a]		
Subfamily Zetoborinae		
Phortioeca phoraspoides	PHRTC	●
Subfamily Blaberinae		
Archimandrita tessellata	ARCHM	●
Blaberus craniifer	BLCRN	●
Blaberus discoidalis	BLDSC	●
Blaberus giganteus	BLGIG	●
Byrsotria fumigata	BYRST	●
Eublaberus posticus	EUBLB	●
Subfamily Panesthiinae		
Panesthia australis	PANST	●
Panchloroin Complex[a]		
Subfamily Pycnoscelinae		
Pycnoscelus indicus	PCNBS	●
Pycnoscelus surinamensis	PCNPR	●
Subfamily Diplopterinae		
Diploptera punctata	DPLPT	●
Subfamily Panchlorinae		
Capucina patula	CAPUC	●
Panchlora nivea	PNCHL	●

TABLE 4. (Continued)

	Abbreviated name	Symbol on plan view of models
Subfamily Oxyhaloinae		
Gromphadorhina portentosa	GRMPH	
Leucophaea maderae	LUCPH	
Nauphoeta cinerea	NAUPH	
Epilamproin Complex[a]		
Subfamily Epilamprinae		
Audreia bromeliadarum	AUDRE	
Hyporhicnoda litomorpha	HYPRH	

[a] McKittrick gave these complexes the suffix -oid, which might confuse them with superfamilies. To avoid this confusion, the endings have been changed to -oin to indicate that the complexes refer to groups of subfamilies.

TABLE 5. Relevant OTU's of McKittrick with abbreviations used in the present study.

Table no. (McKittrick, 1964)	OTU	Abbreviated name
1	Blaberinae	BLABER
	Blattellinae	BLATEL
	Blattinae	BLATTN
	Cryptocercinae	CRYPTO
	Diplopterinae	DIPLOP
	Epilamprinae	EPILAM
	Lamproblattinae	LAMPRO
	Oxyhaloinae	OXYHAL
	Panchlorinae	PANCHL
	Panesthiinae	PANEST
	Plectopterinae	PLECTO
	Polyphaginae	POLYPH
	Polyzosteriinae	POLYZO
	Pycnoscelinae	PYCNOS
	Zetoborinae	ZETBOR
4	*Arenivaga bolliana* (Saussure)	ARNVBL
4, 5	*Parcoblatta virginica* (Brunner)	PRCBVA
6, 7	*Pycnoscelus*—not certain whether *P. indicus* or *P. surinamensis* was used	PCN
	Audreia cicatricosa (Rehn)	AUDRCC
	Panesthia angustipennis (Illiger)	PNSTAN

TABLE 6. Cophenetic correlations among the matrices of the female stages.

		Distances		
		Small nymph	Large nymph	Adult
Correlations	Small nymph	—	.548	.406
	Large nymph	.565	—	.762
	Adult	.553	.787	—

TABLE 7. Cophenetic correlations among the matrices of the male stages.

		Distances		
		Small nymph	Large nymph	Adult
Correlations	Small nymph	—	.524	.479
	Large nymph	.586	—	.765
	Adult	.541	.818	—

TABLE 8. Cophenetic correlations among the correlation matrices between the sexes.

		Males		
		Small nymph	Large nymph	Adult
Females	Small nymph	.940	.571	.523
	Large nymph	.564	.879	.758
	Adult	.572	.762	.843

TABLE 9. Cophenetic correlations among the distance matrices between the sexes.

		Males		
		Small nymph	Large nymph	Adult
Females	Small nymph	.976	.533	.502
	Large nymph	.580	.894	.707
	Adult	.436	.683	.747

TABLE 10. Cophenetic correlations among centroid distance matrices within each sex.

		Males		
		Small nymph	Large nymph	Adult
Females	Small nymph	—	.564	.591
	Large nymph	.605	—	.802
	Adult	.487	.830	—

TABLE 11. Cophenetic correlations among centroid distance matrices between sexes.

		Males		
		Small nymph	Large nymph	Adult
Females	Small nymph	.969	.574	.581
	Large nymph	.637	.878	.705
	Adult	.541	.737	.768

FIGURE LEGENDS

For keys to the abbreviations and symbols used in the Figures, see Tables 4 and 5. Several species are represented in the cases where an OTU is identified not by an abbreviation, but by a generic name alone. Where the members of a subfamily do not all cluster together in the phenograms, the subfamily name is followed by an asterisk. The abbreviation NCHAR refers to the number of characters, and r_{coph} to the cophenetic correlation coefficient.

Except as noted, the models were photographed from the negative side of the first axis (top to bottom of the page). Axis II runs from left to right and axis III is vertical. The positions of OTU's hidden by others in the photographs can be determined by referring to the accompanying 2-dimensional graphs. In these Figures (except for Fig. 3), 1 major grid unit=2 projection units.

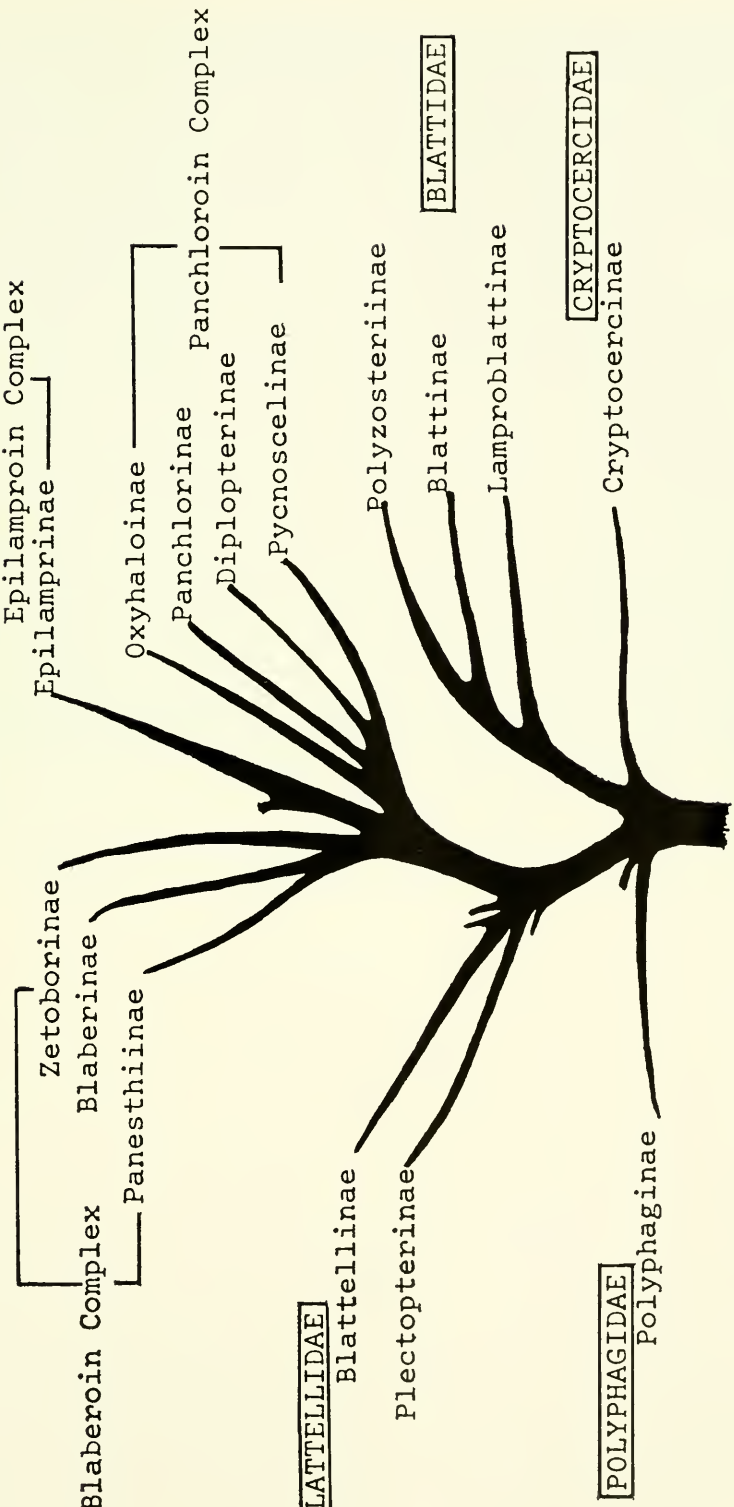


Fig. 1. Phylogram of the familes and subfamilies of the Blattaria after McKittrick's "Text Figure 1."

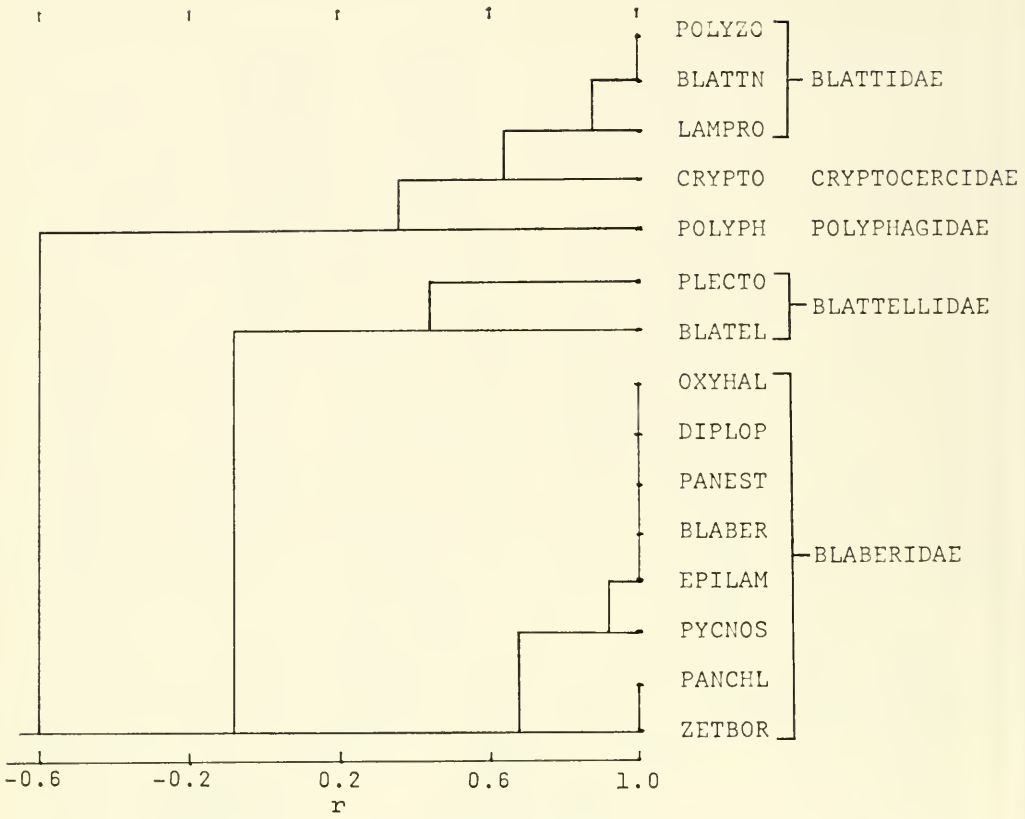


FIG. 2. Phenogram of correlation coefficients among the subfamilies of the Blattaria, from McKittrick's Table 1. NCHAR=46. r_{coph}=0.974.

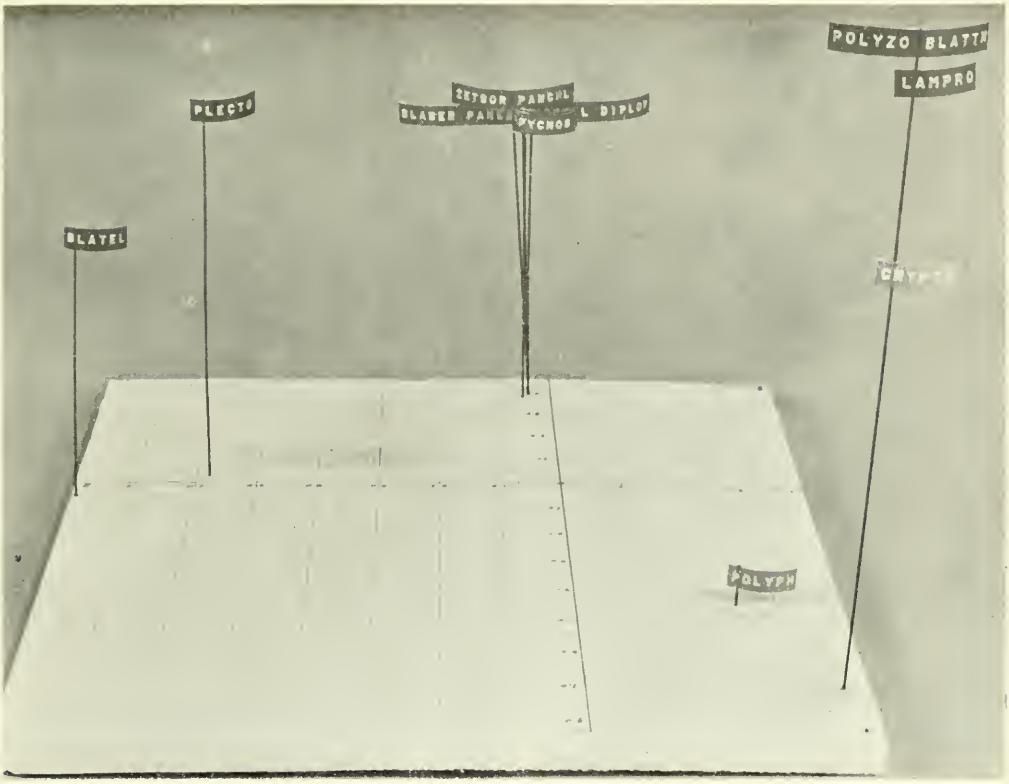


FIG. 3. Centroid component analysis of the subfamilies of the Blattaria, from McKittrick's Table 1. Model viewed from positive side of axis I. Scale: 1 major grid unit=1 projection unit. PYCNOS obscures EPILAM and also the coordinate point shared by BLABER, PANEST, OXYHAL, and DIPLOP. NCHAR=46. r_{coph}=0.987. Factor I=54.0%, II=21.4%, III=9.0% of total variance. Total extracted variance=84.4%.

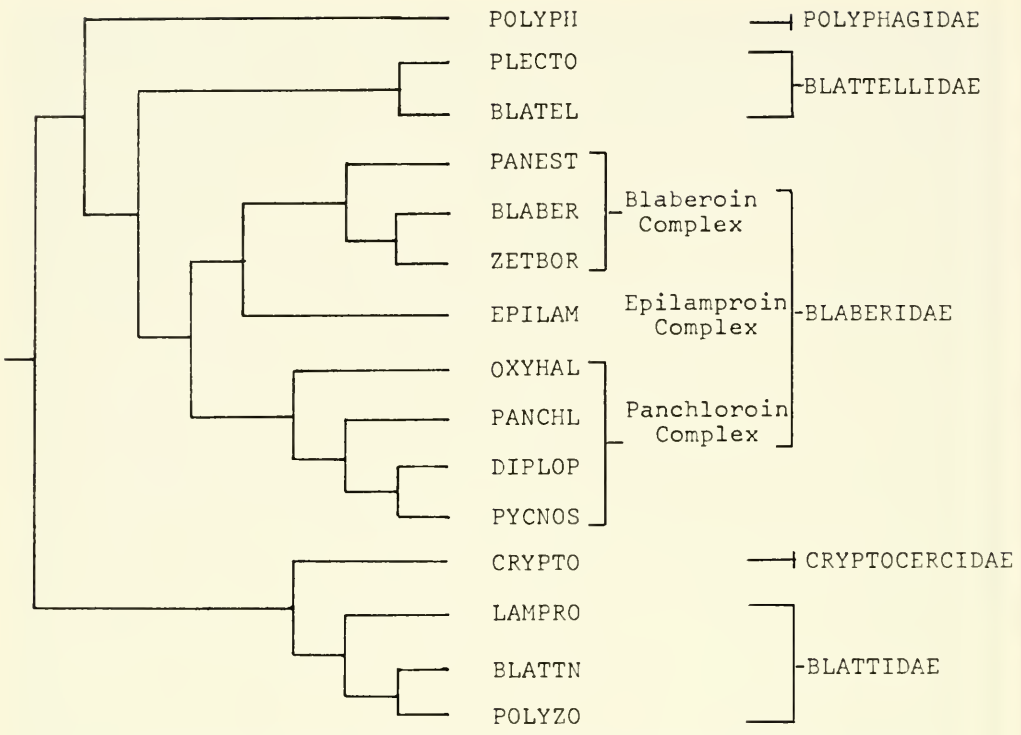


FIG. 4. Interpretive phenogram of the families and subfamilies of the Blattaria, from Figure 1.

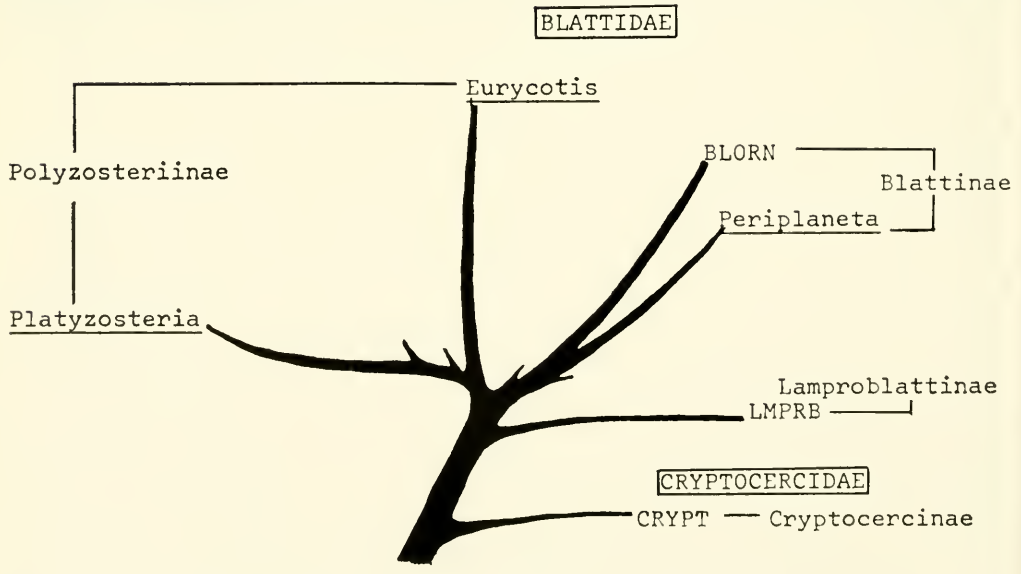
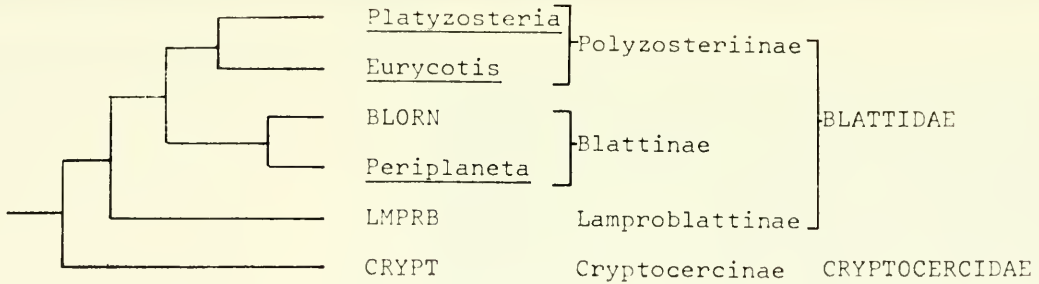


FIG. 5. Phylogram of the Cryptocercidae and Blattidae, after McKittrick's "Text Figure 2."



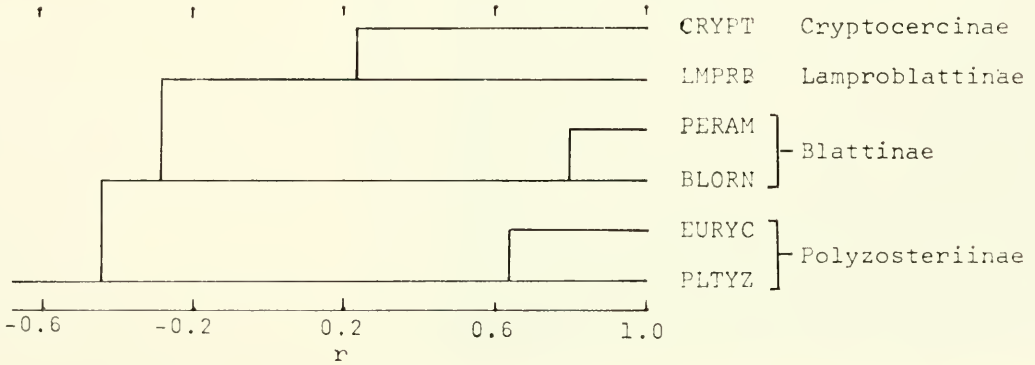


FIG. 6 (above). Interpretive phenogram of the Cryptocercidae and Blattidae, from Figure 5.

FIG. 7 (below). Phenogram of correlation coefficients among the Cryptocercidae and Blattidae, from McKittrick's Table 2. NCHAR=32. r_{coph}=0.978.

FIG. 8. Centroid component analysis of the Cryptocercidae and Blattidae, from McKittrick's Table 2. Model viewed from positive side of axis I. NCHAR=32. r_{coph}=0.958. Factor I=45.9%, II=30.6%, III=13.3% of total variance. Total extracted variance=89.8%.

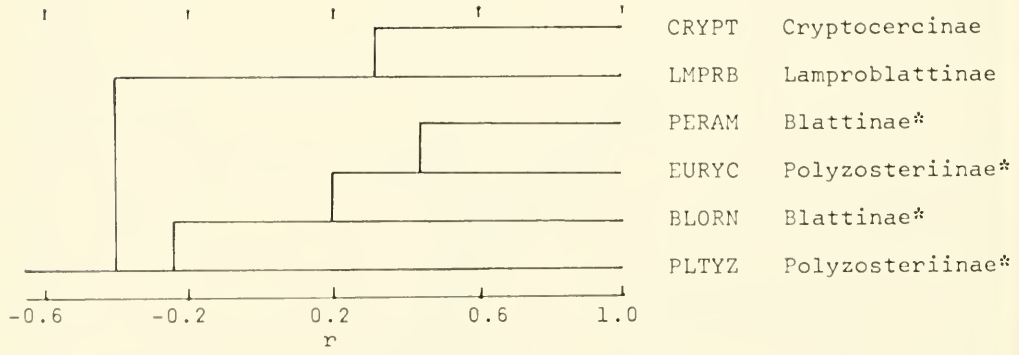


FIG. 9. Phenogram of correlation coefficients among the Cryptocercidae and Blattidae, from McKittrick's Table 3. NCHAR=24. r_{coph}=0.965.

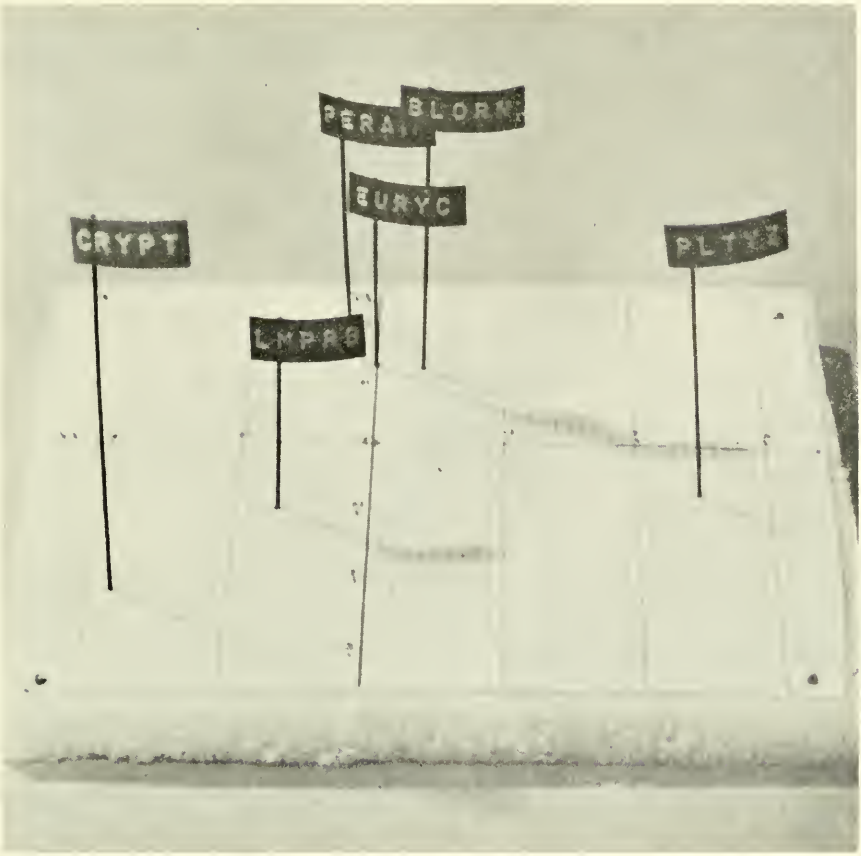


FIG. 10. Centroid component analysis of the Cryptocercidae and Blattidae, from McKittrick's Table 3. Model viewed from negative side of axis II. NCHAR=24. r_{coph}=0.921. Factor I=32.7%, II=37.6%, III=11.9% of total variance. Total extracted variance=82.2%.

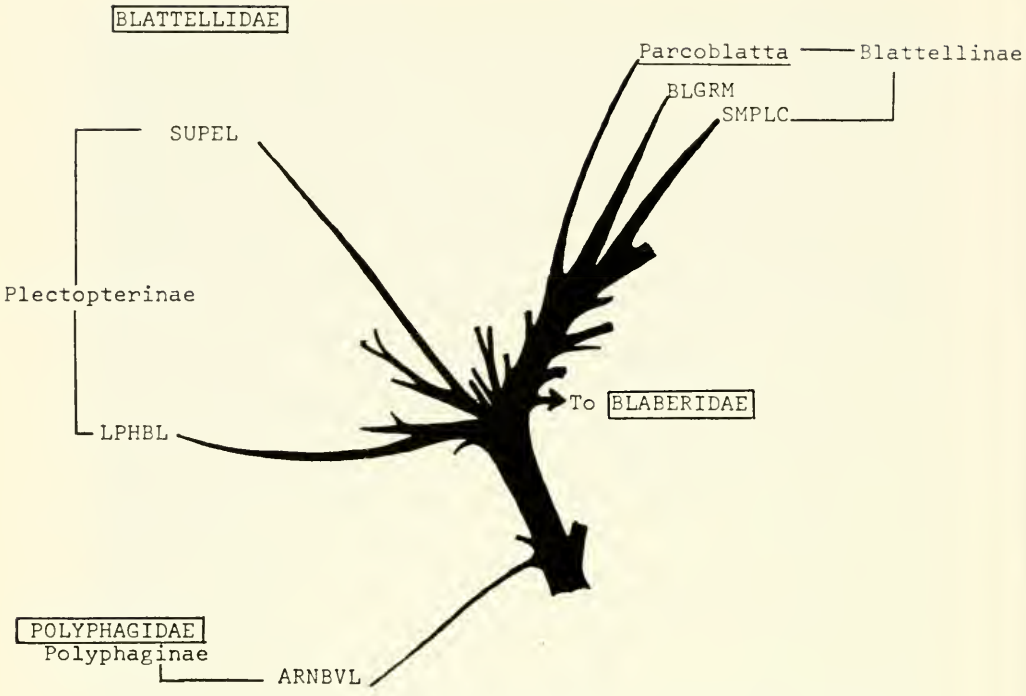
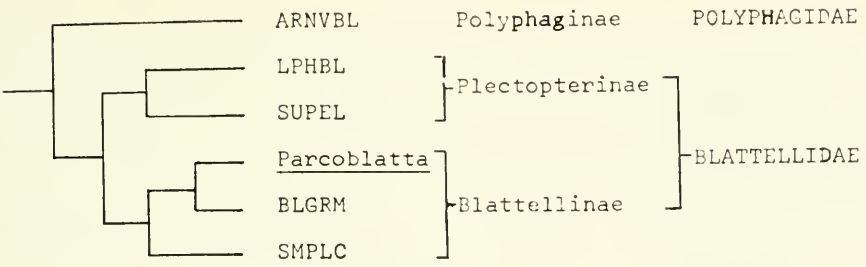
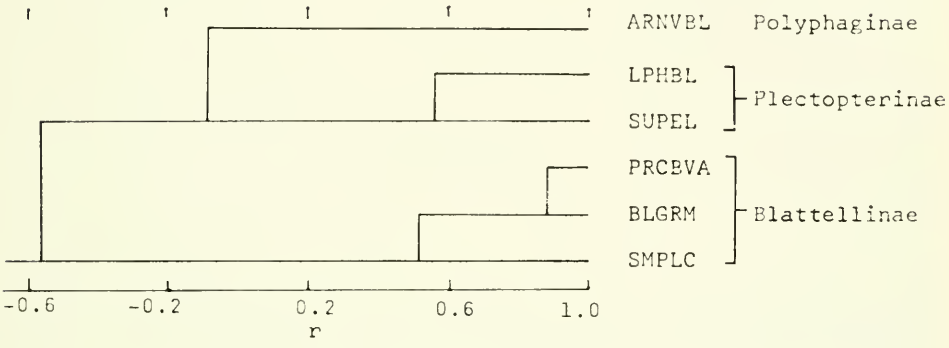


FIG. 11. Phylogram of the Polyphagidae and Blattellidae, after McKittrick's "Text Figure 3."





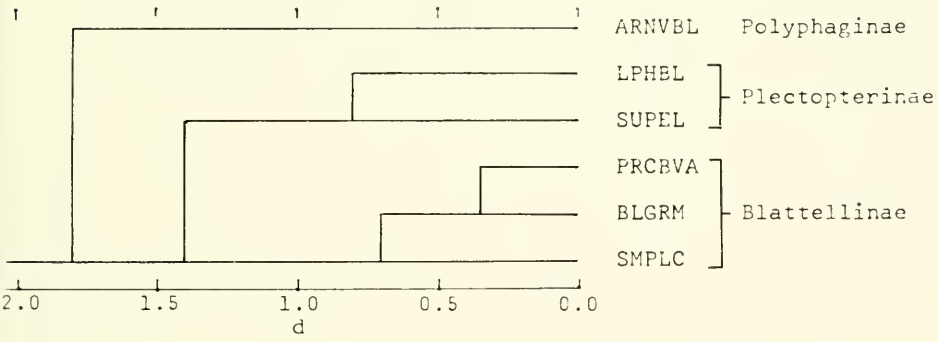
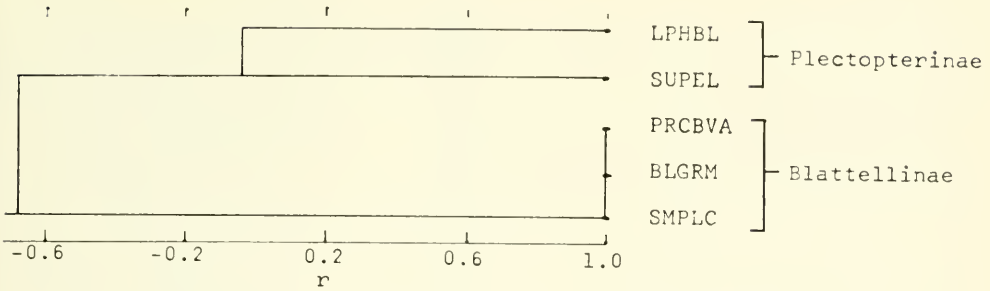


FIG. 12 (above). Interpretive phenogram of the Polyphagidae and Blattellidae, from Figure 11.

FIG. 13 (center). Phenogram of correlation coefficients among the Polyphagidae and Blattellidae, from McKittrick's Table 4. NCHAR=30. r_{coph}=0.996.

FIG. 14 (below). Phenogram of distance coefficients among the Polyphagidae and Blattellidae, from McKittrick's Table 4. NCHAR=30. r_{coph}=0.995.

FIG. 15. Centroid component analysis of the Polyphagidae and Blattellidae, from McKittrick's Table 4. NCHAR=30. r_{coph}=0.991. Factor I=34.9%, II=50.7%, III=7.9% of total variance. Total extracted variance=93.5%.



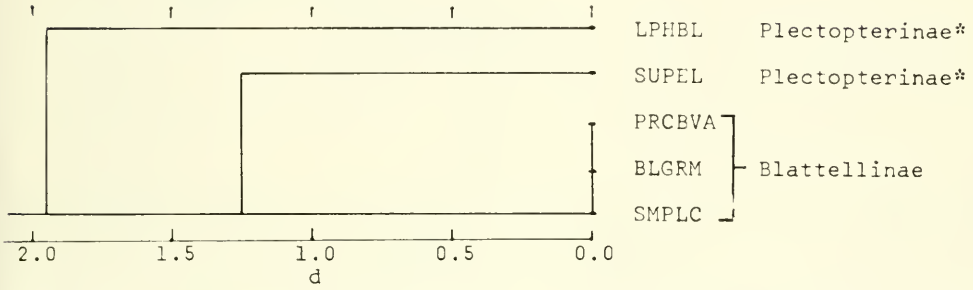


FIG. 16 (above). Phenogram of correlation coefficients among the Blattellidae, from McKittrick's Table 5. NCHAR=16. r_{coph}=0.985.

FIG. 17 (below). Phenogram of distance coefficients among the Blattellidae, from McKittrick's Table 5. NCHAR=16. r_{coph}=0.997.

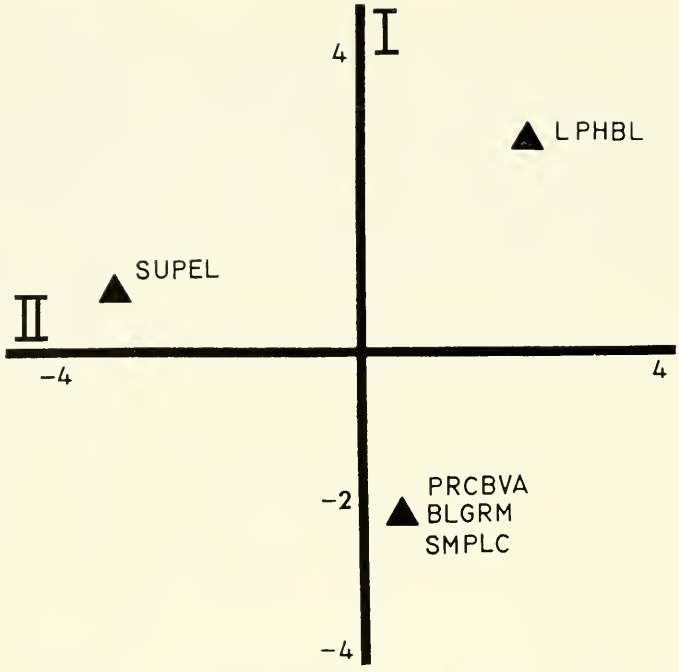


FIG. 18. Centroid component analysis of the Blattellidae, from McKittrick's Table 5. This model is two-dimensional because the total variance can be expressed by two factors. NCHAR=16. r_{coph}=0.998. Factor I=76.1%, II=23.9% of total variance.

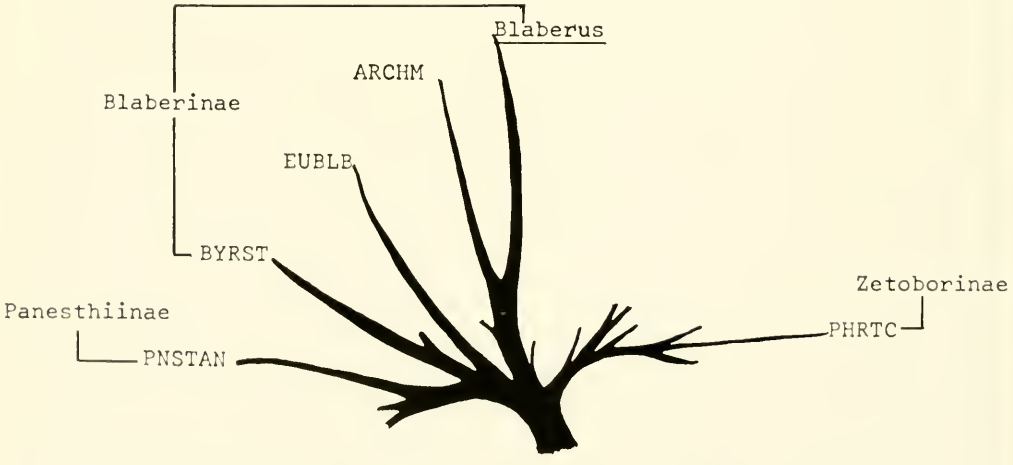


FIG. 19. Phylogram of the blaberoin complex of the Blaberidae, after McKittrick's "Text Figure 4."

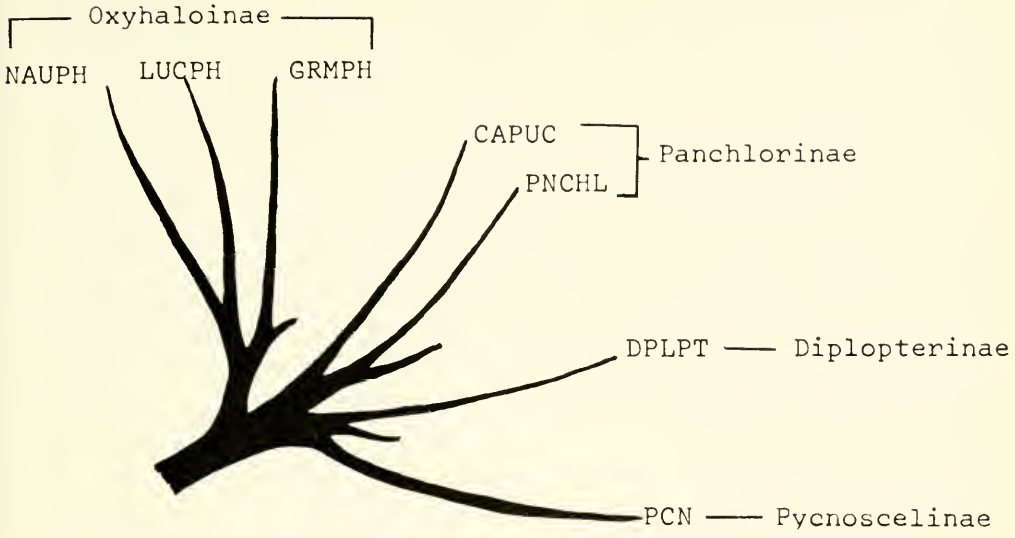


FIG. 20. Phylogram of the panchloroin complex of the Blaberidae, after McKittrick's "Text Figure 5."

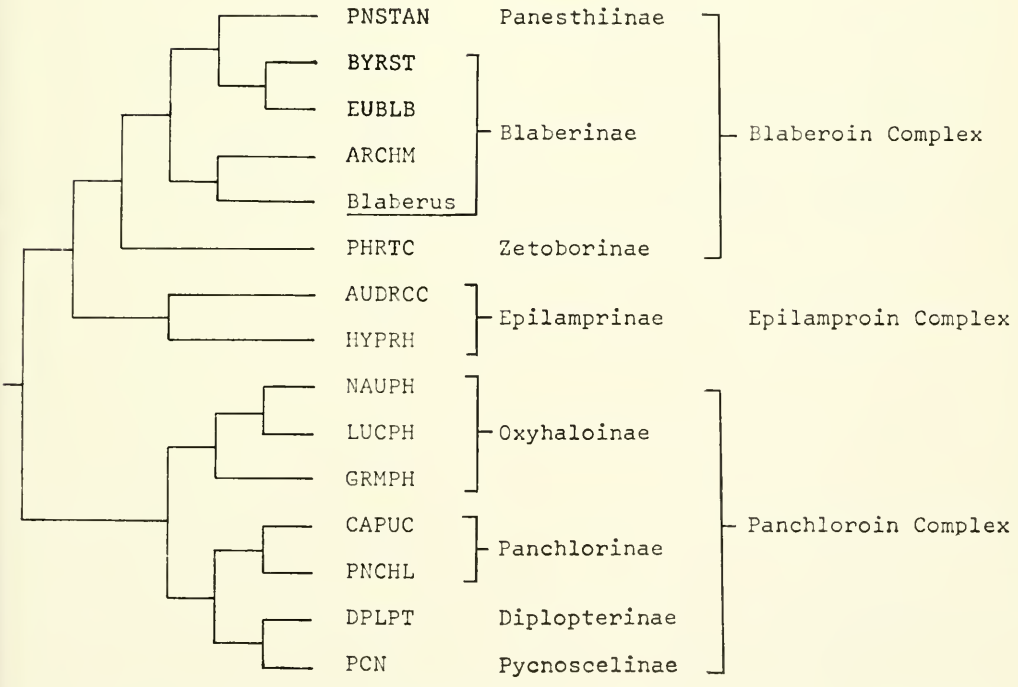


FIG. 21. Interpretive phenogram of the Blaberidae, from a combination of Figures 19 and 20 and the epilamproin OTU's.

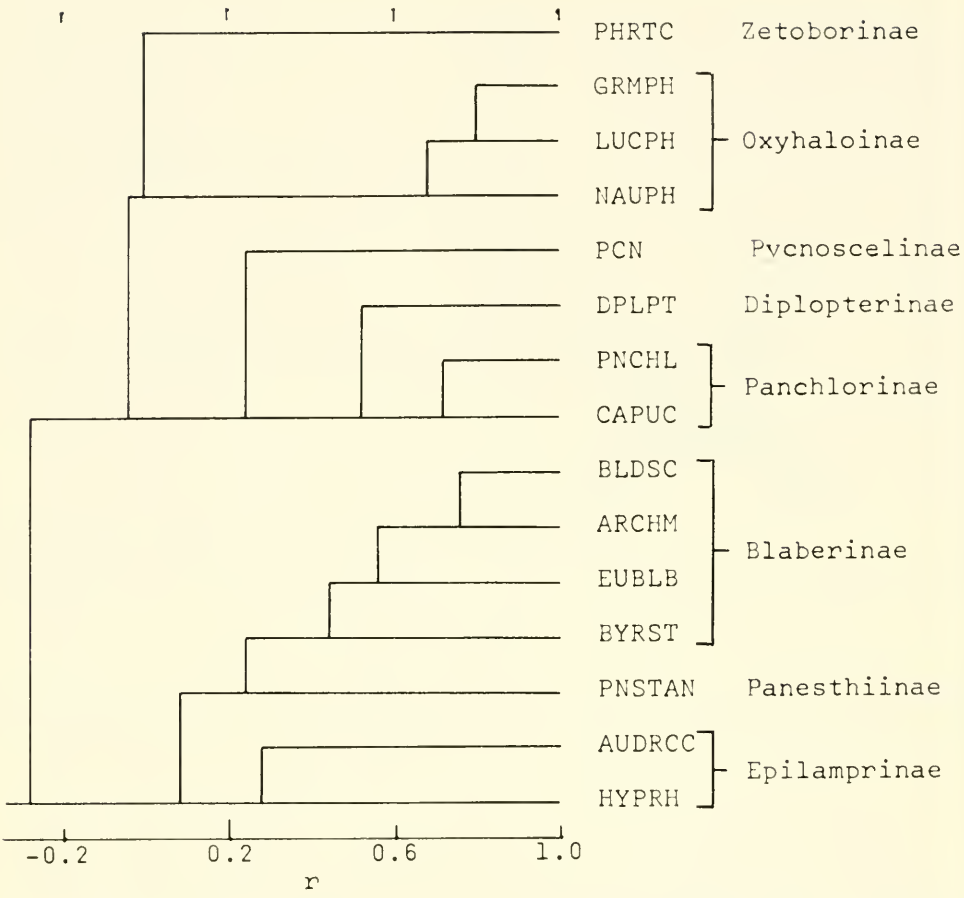


FIG. 22. Phenogram of correlation coefficients among the Blaberidae, from McKittrick's Table 6. NCHAR=30. r_{coph}=0.908.

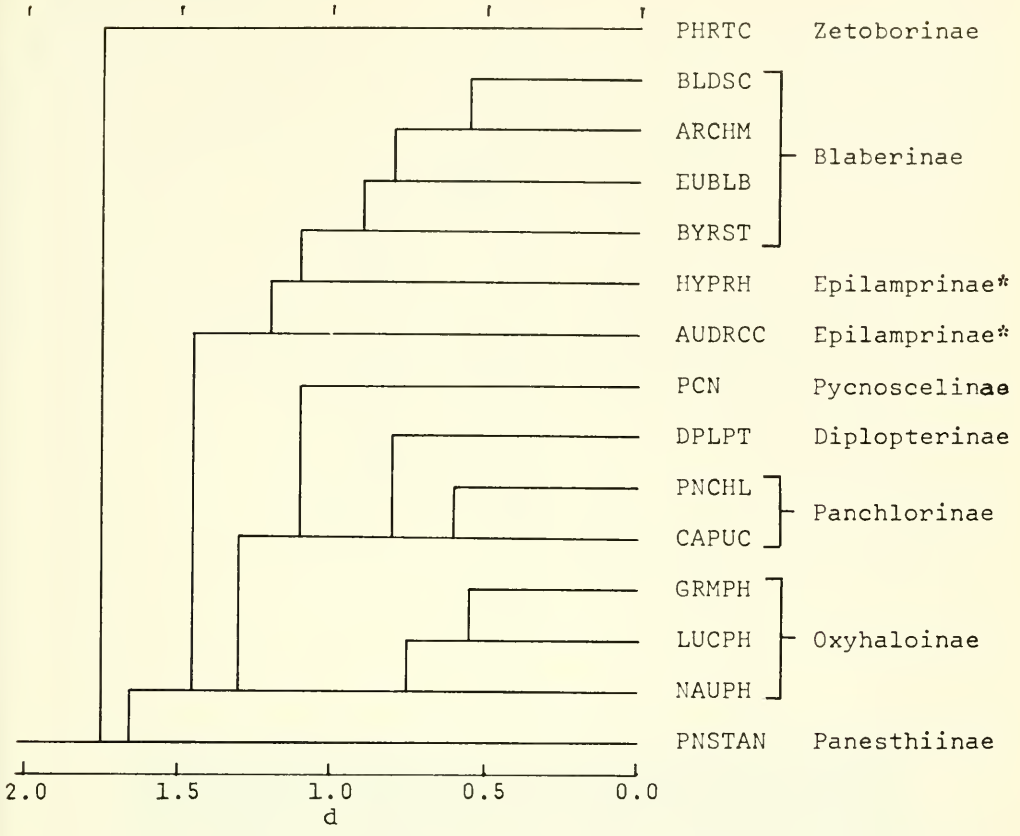


FIG. 23. Phenogram of distance coefficients among the Blaberidae, from McKittrick's Table 6. NCHAR=30. r_{coph}=0.914.

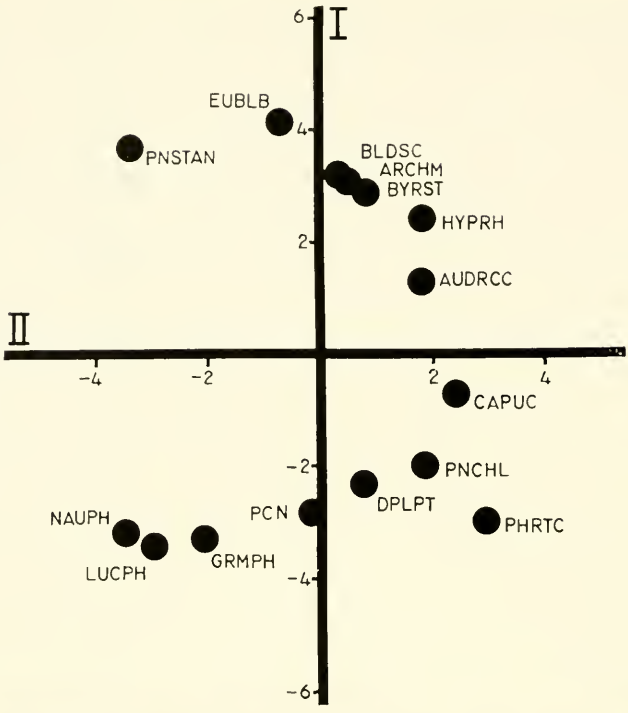


FIG. 24. Centroid component analysis of the Blaberidae, from McKittrick's Table 6. Two-dimensional diagram and three-dimensional model. NCHAR=30. r_{coph}=0.904. Factor I=29.5%, II=14.8%, III=11.8% of total variance. Total extracted variance=56.1%.

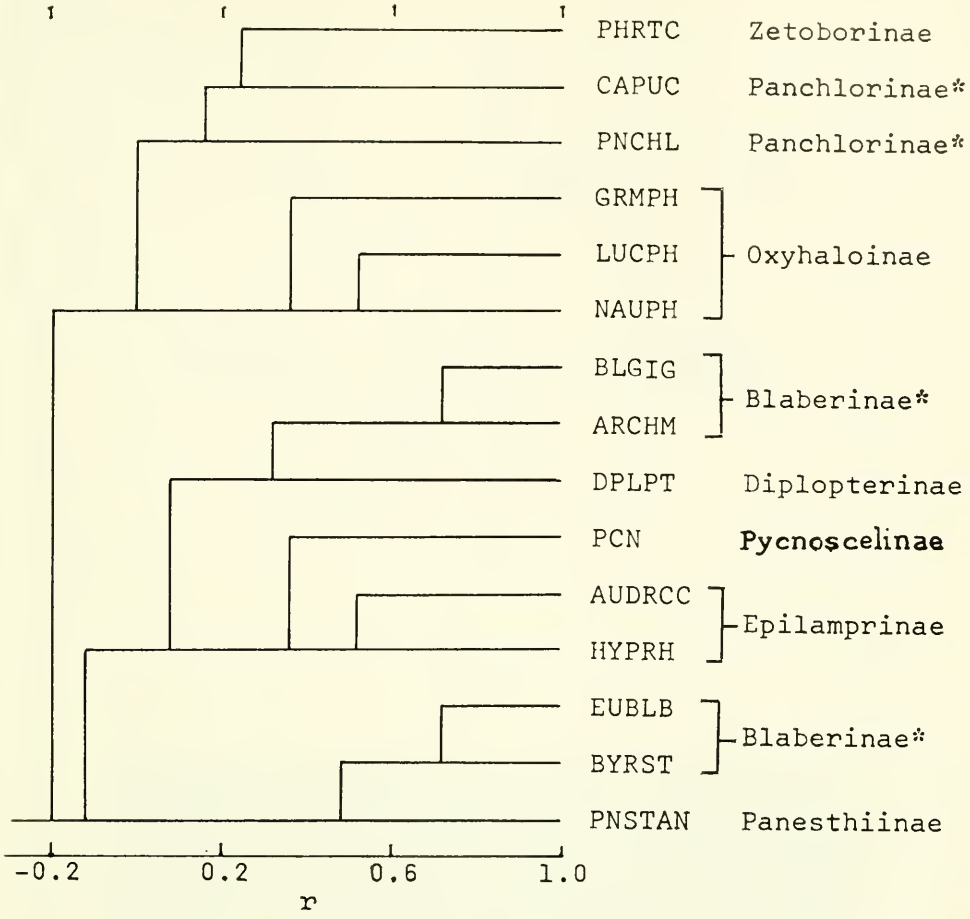


FIG. 25. Phenogram of correlation coefficients among the Blaberidae, from McKittrick's Table 7. NCHAR=33. r_{coph}=0.870.

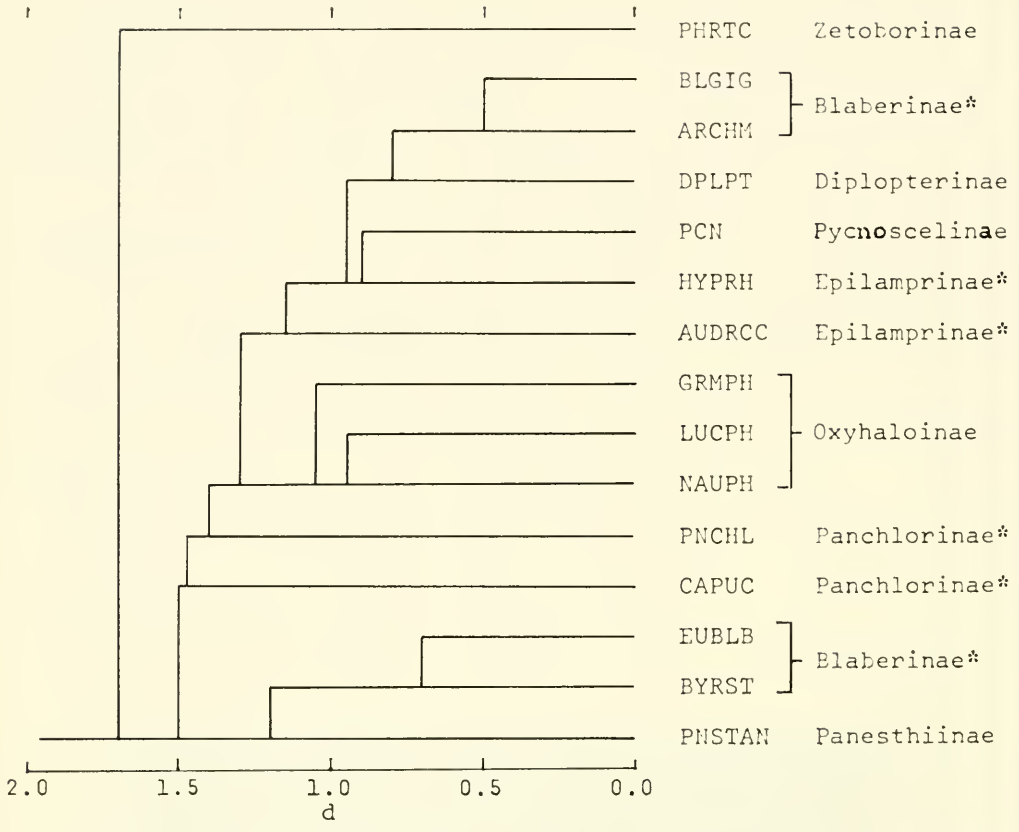
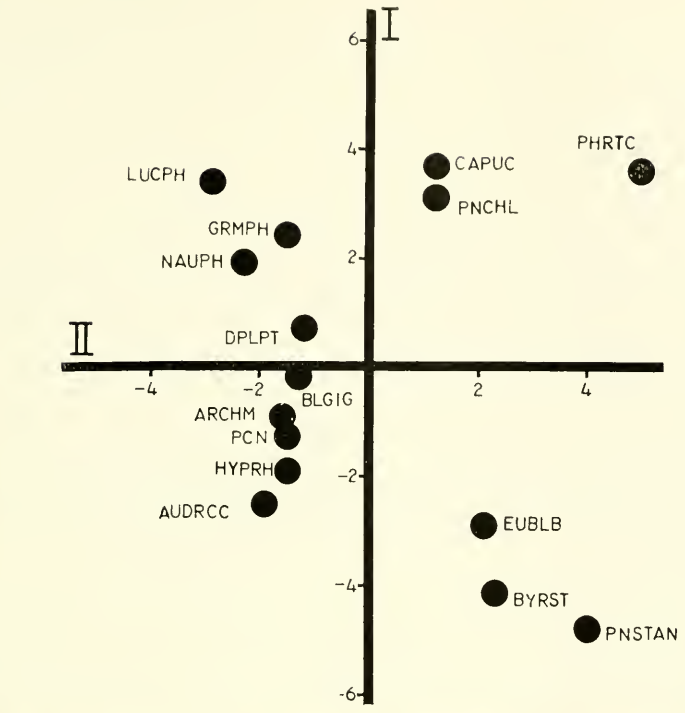


FIG. 26. Phenogram of distance coefficients among the Blaberidae, from McKittrick's Table 7. NCHAR=33. r_{coph}=0.809.



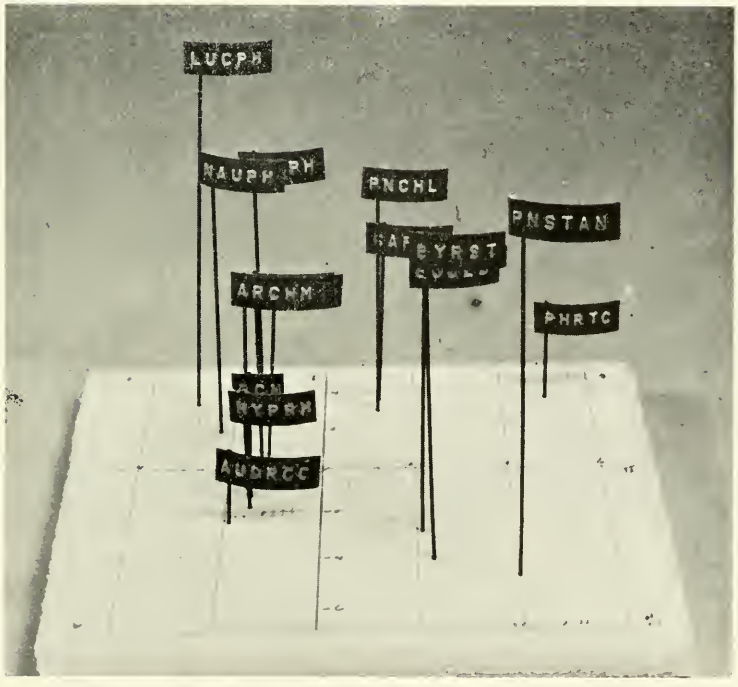
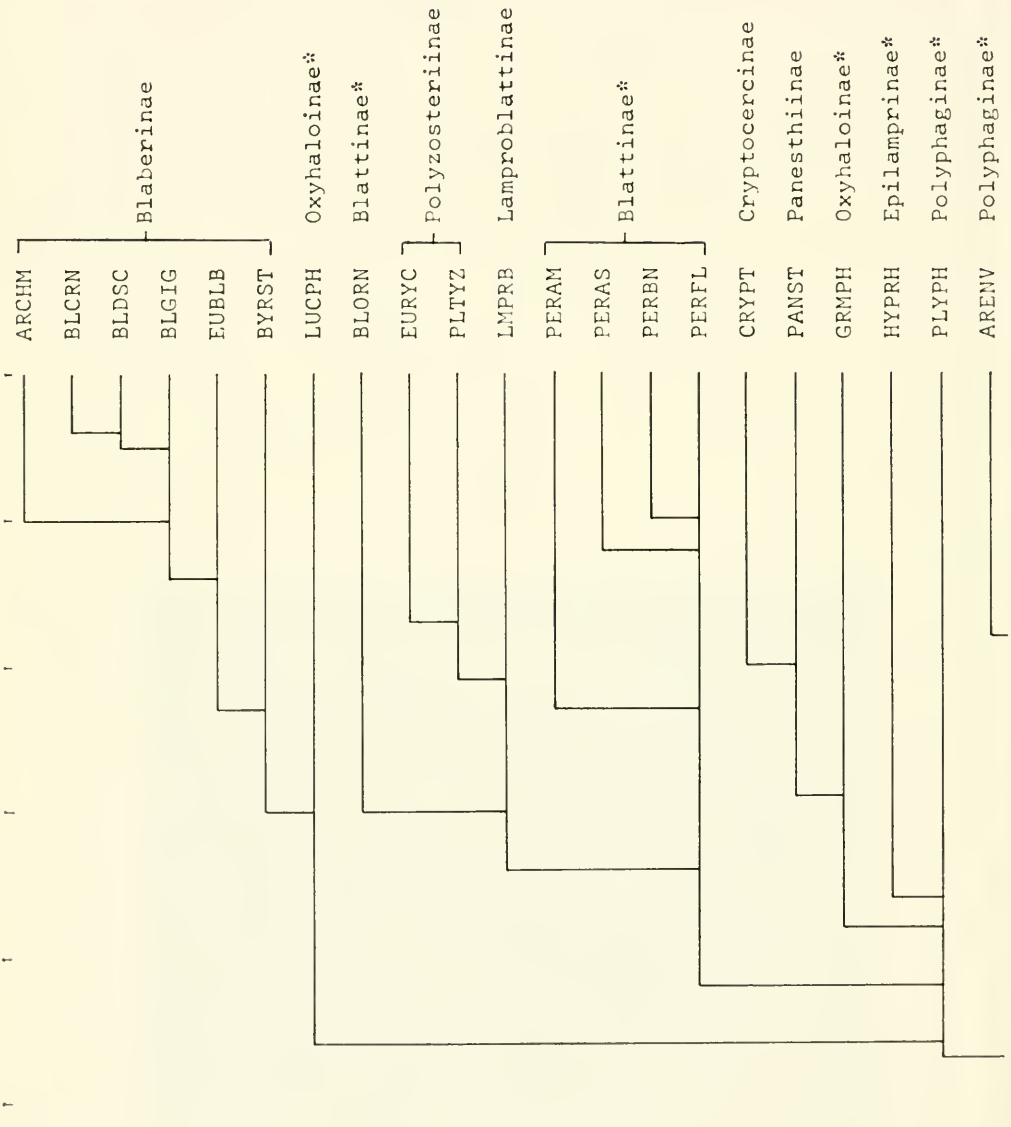


FIG. 27. Centroid component analysis of the Blaberidae, from McKittrick's Table 7. Two-dimensional diagram and three-dimensional model. NCHAR=33. r_{coph}=0.831. Factor I=25.0%, II=17.5%, III=13.0% of total variance. Total extracted variance=55.5%.


ARCHM
BLCRN
BLDSC
Blaberinae
BLGIG
EUBLB
BYRST
LUCPH Oxyhaloinae*
BLORN Blattinae*
EURYC
Polyzosterinae
PLTYZ
LMPRB Lamproblattinae
PERAM
PERAS
Blattinae*
PERBN
PERFL
CRYPT Cryptocercinae
PANST Panesthiinae
GRMPH Oxyhaloinae*
HYPRH Epilamprinae*
PLYPH Polyphaginae*
ARENV Polyphaginae*

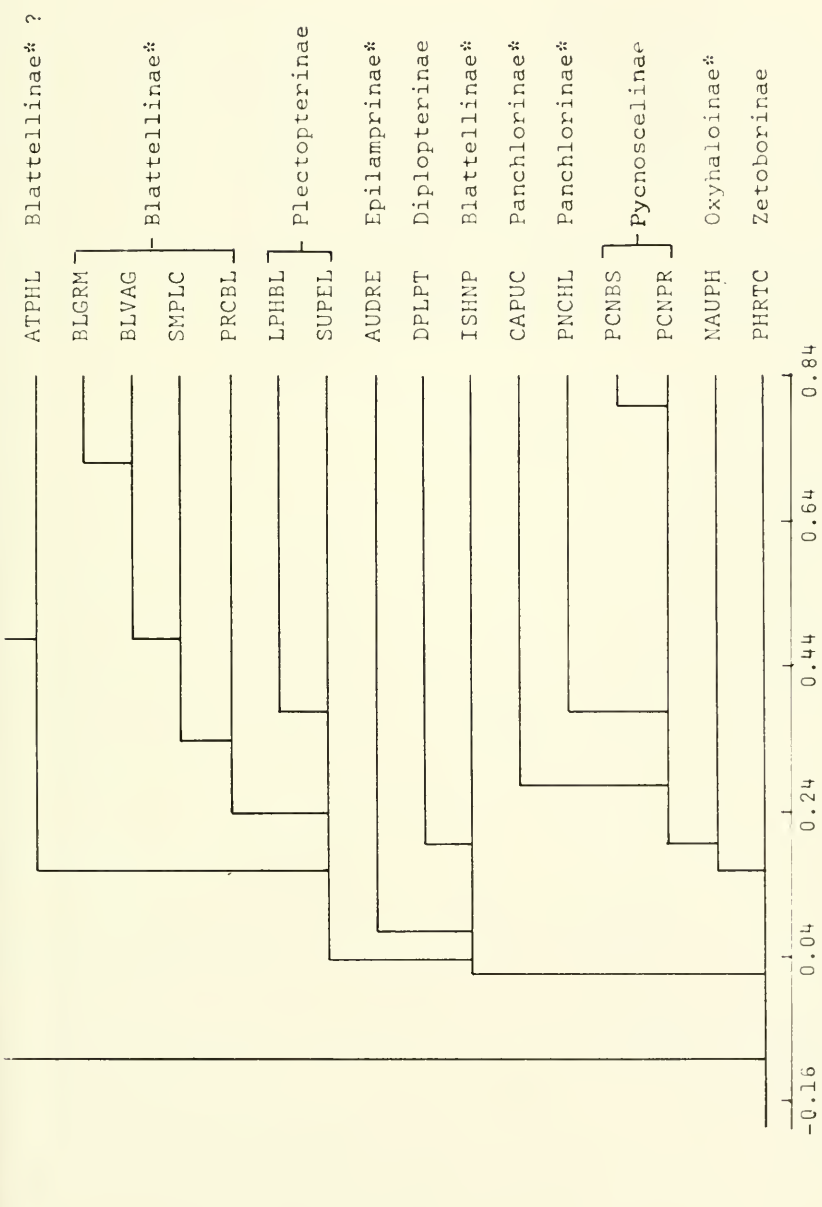
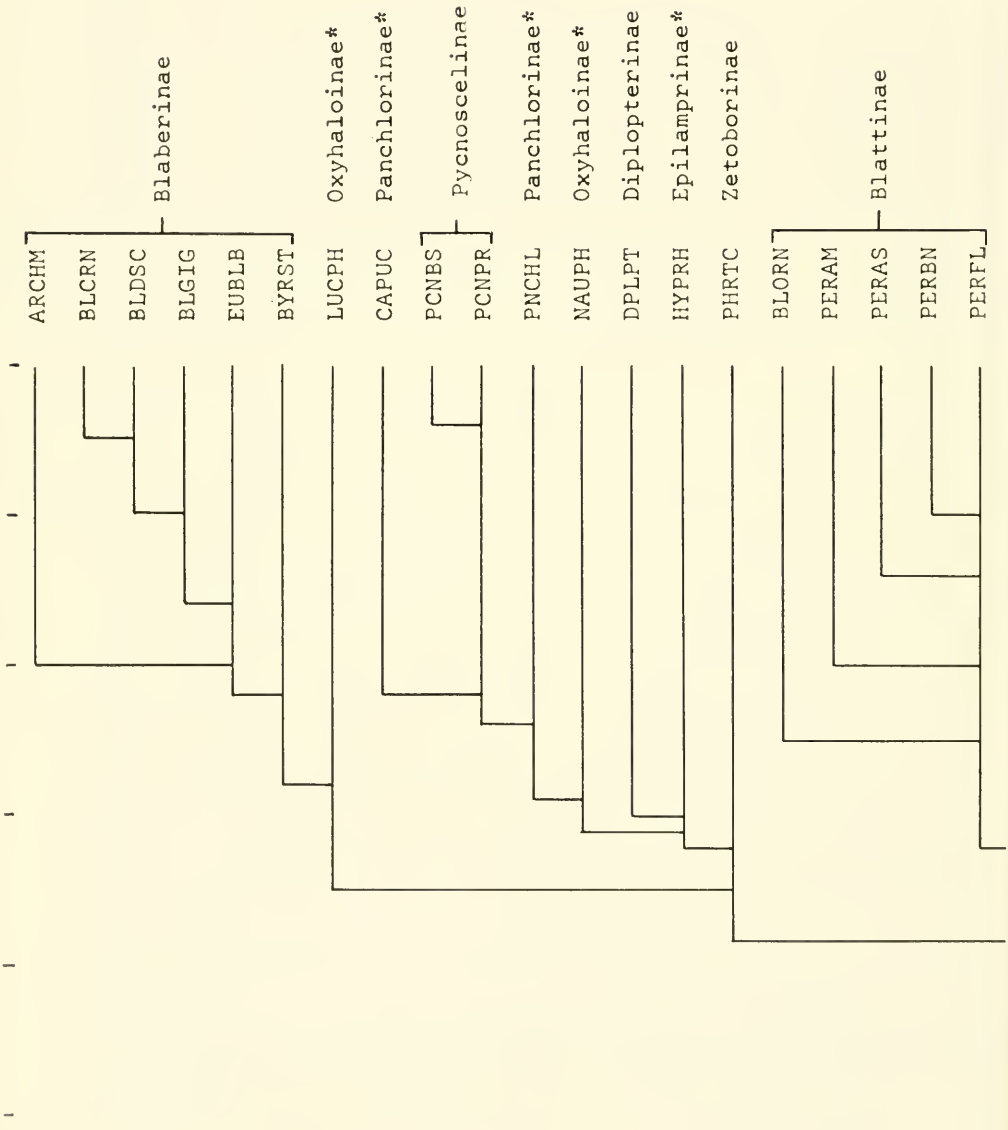


FIG. 28. Phenogram of correlation coefficients among "combined" OTU's of the adults. NCHAR=723. r_{coph}=0.801.


ARCHM
BLCRN
BLDSC
BLGIG
EUBLB
BYRST
LUCPH
CAPUC
PCNBS
PCNPR
PNCHL
NAUPH
DPLPT
HYPRH
PHRTC
BLORN
PERAM
PERAS
PERBN
PERFL
Blaberinae
Oxyhaloinae*
Panchlorinae*
Pycnoscelinae
Panchlorinae*
Oxyhaloinae*
Diplopterinae
Epilamprinae*
Zetoborinae
Blattinae

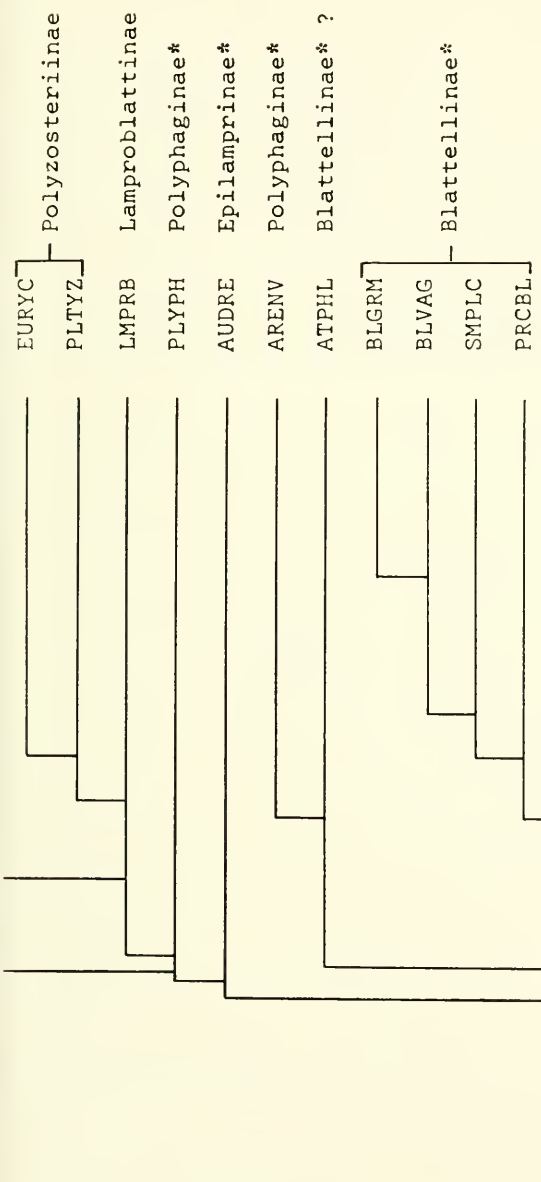
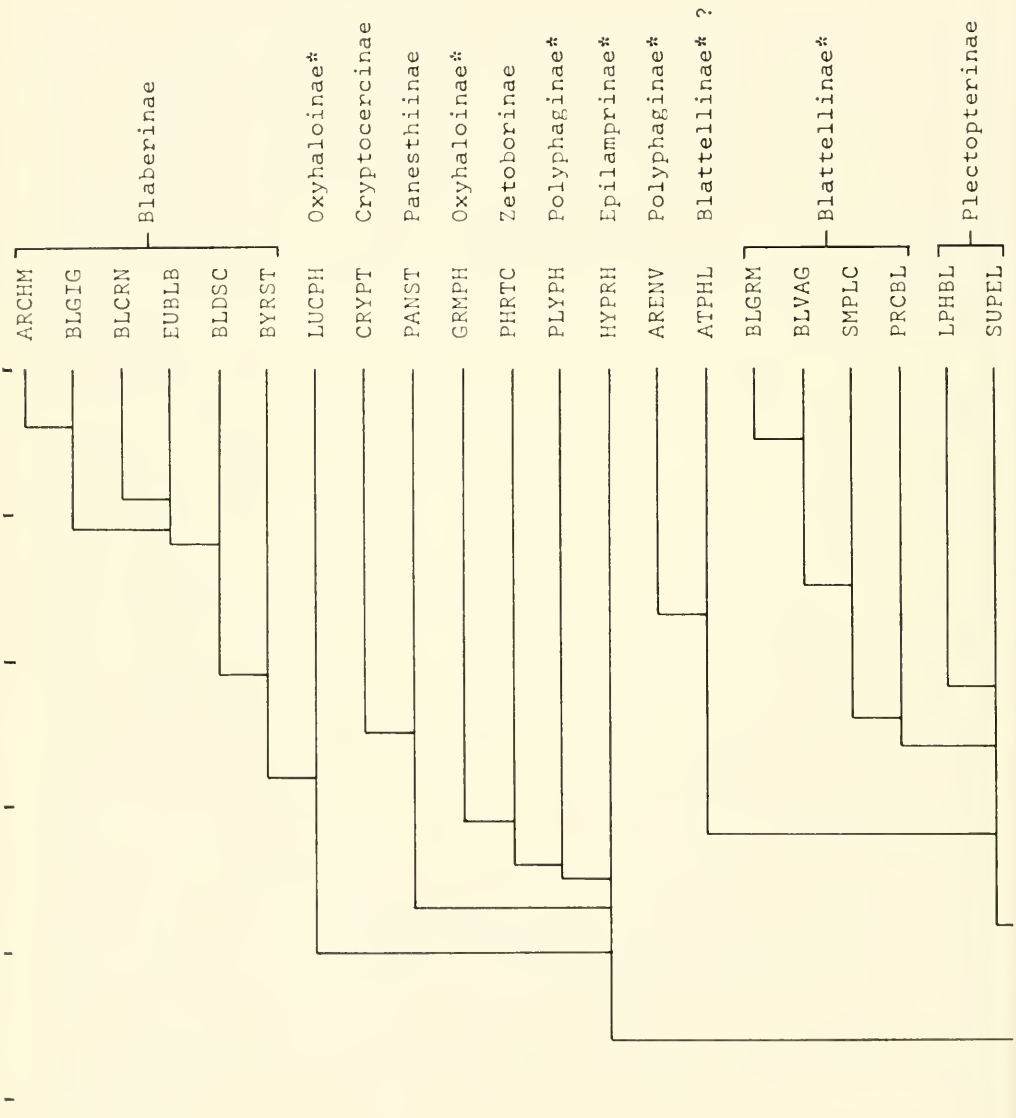


FIG. 29. Phenogram of distance coefficients among "combined" OTU's of the adults. NCHAR=723. r_{coph}=0.757.


ARCHM
BLGIG
BLCRN
EUBLB
BLDSC
BYRST
Blaberinae
LUCPH
Oxyhaloinae*
CRYPT
Cryptocercinae
PANST
Panesthiinae
GRMPH
Oxyhaloinae*
PHRTC
Zetoborinae
PLYPH
Polyphaginae*
HYPRH
Epilamprinae*
ARENV
Polyphaginae*
ATPHL
Blattellinae* ?
BLGRM
BLVAG
SMPLC
PRCBL
Blattellinae*
LPHBL
SUPEL
Plectopterinae

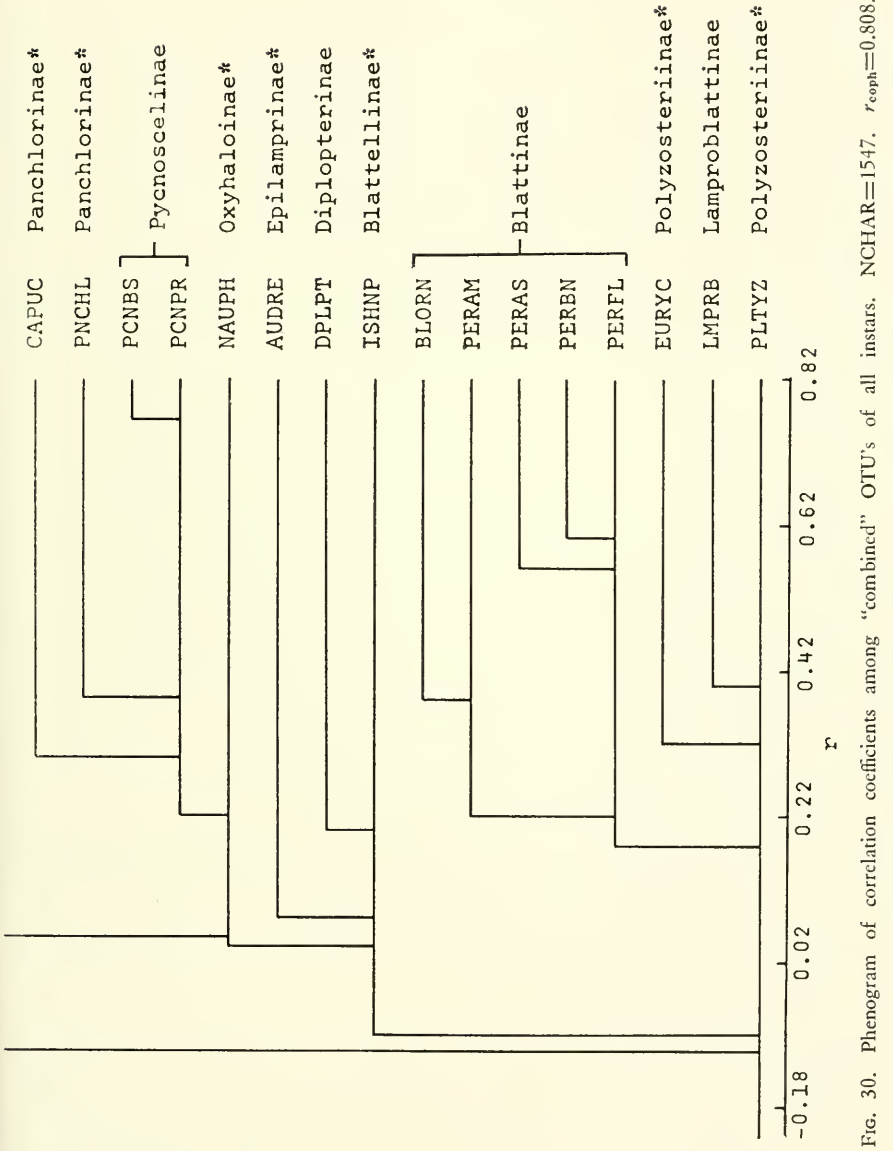
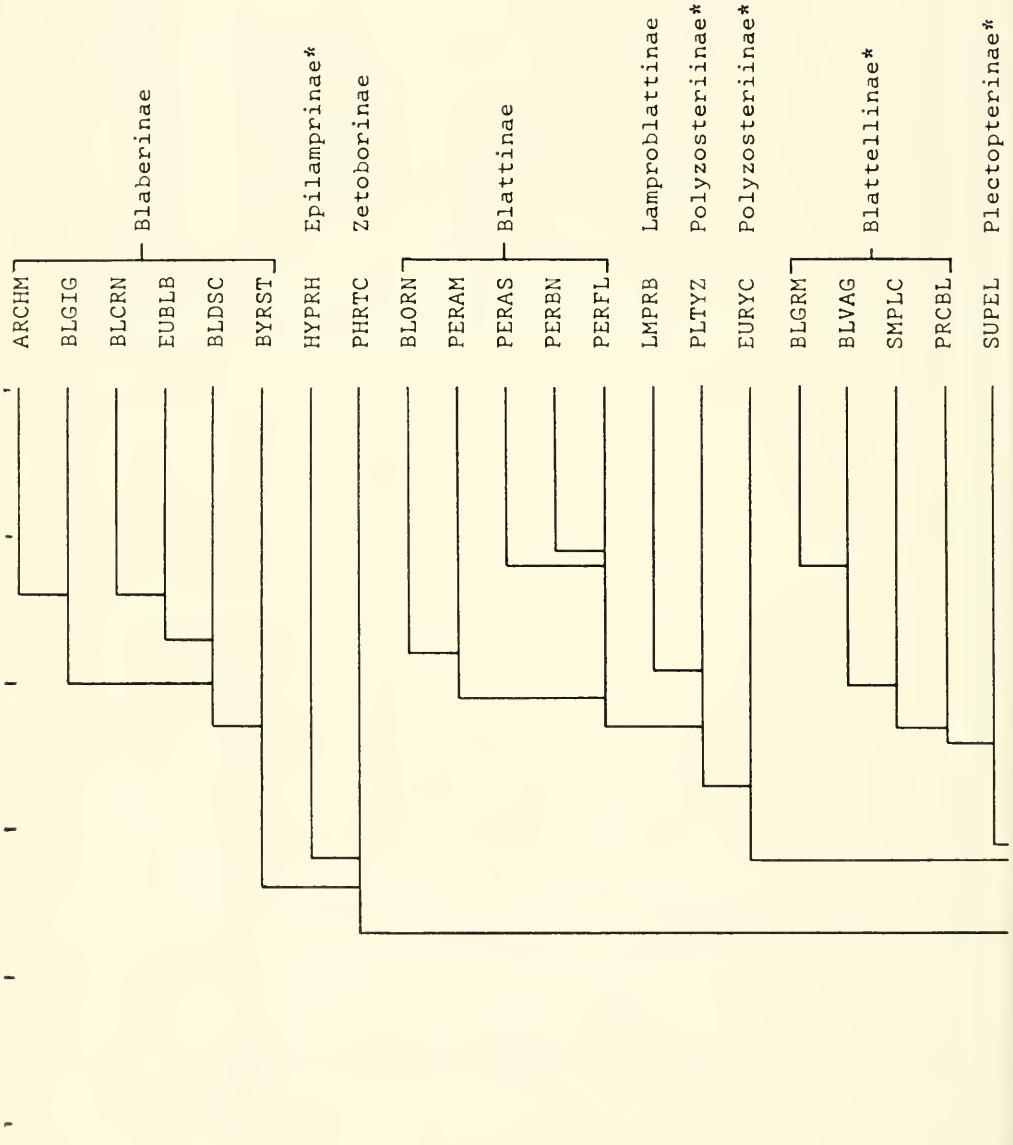


FIG. 30. Phenogram of correlation coefficients among "combined" OTU's of all instars. NCHAR=1547. r_{coph}=0.808.


ARCHM
BLGIG
BLCRN
EUBLB
BLDSC
BYRST
Blaberinae
HYPRH
PHRTC
Epilamprinae*
Zetoborinae
BLORN
PERAM
PERAS
PERBN
PERFL
Blattinae
LMPRB
Lamproblattinae
PLTYZ
Polyzosteriinae*
EURYC
Polyzosterilinae*
BLGRM
BLVAG
SMPLC
PRCBL
Blattellinae*
SUPEL
Plectopterinae*

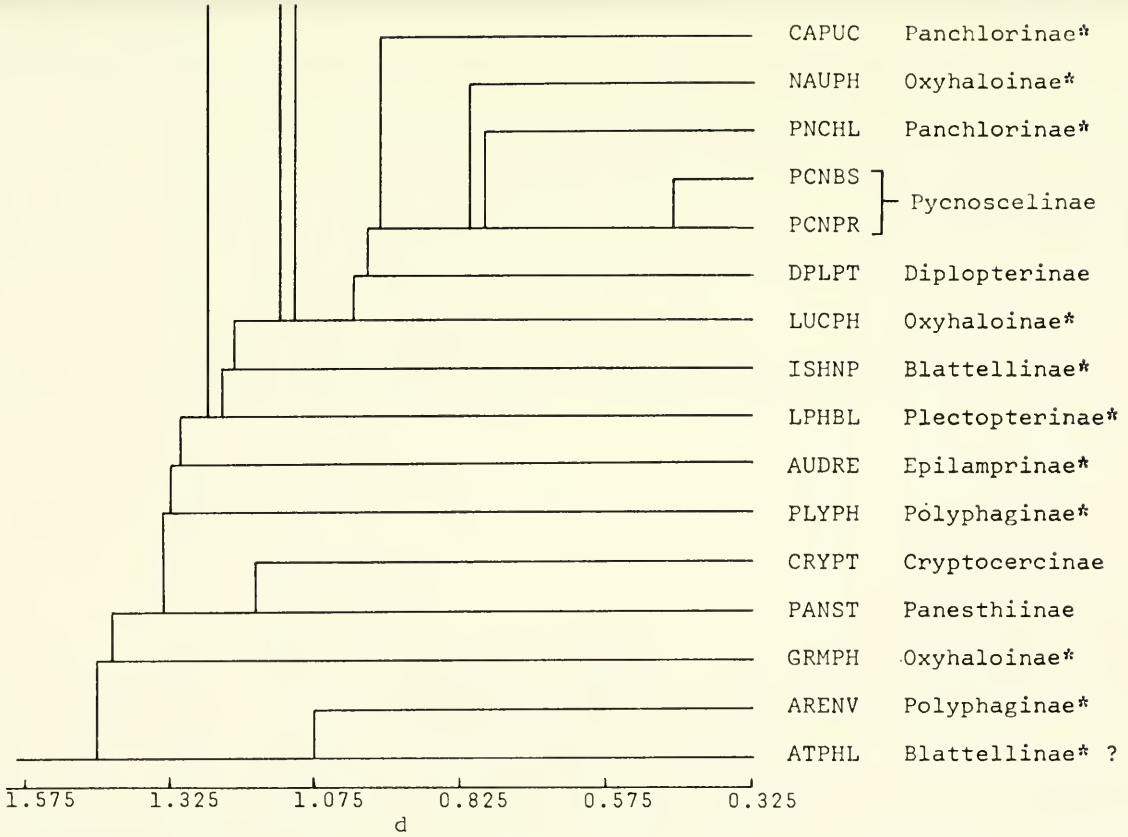


FIG. 31. Phenogram of distance coefficients among "combined" OTU's of all instars. NCHAR=1547. r_{coph}=0.779.

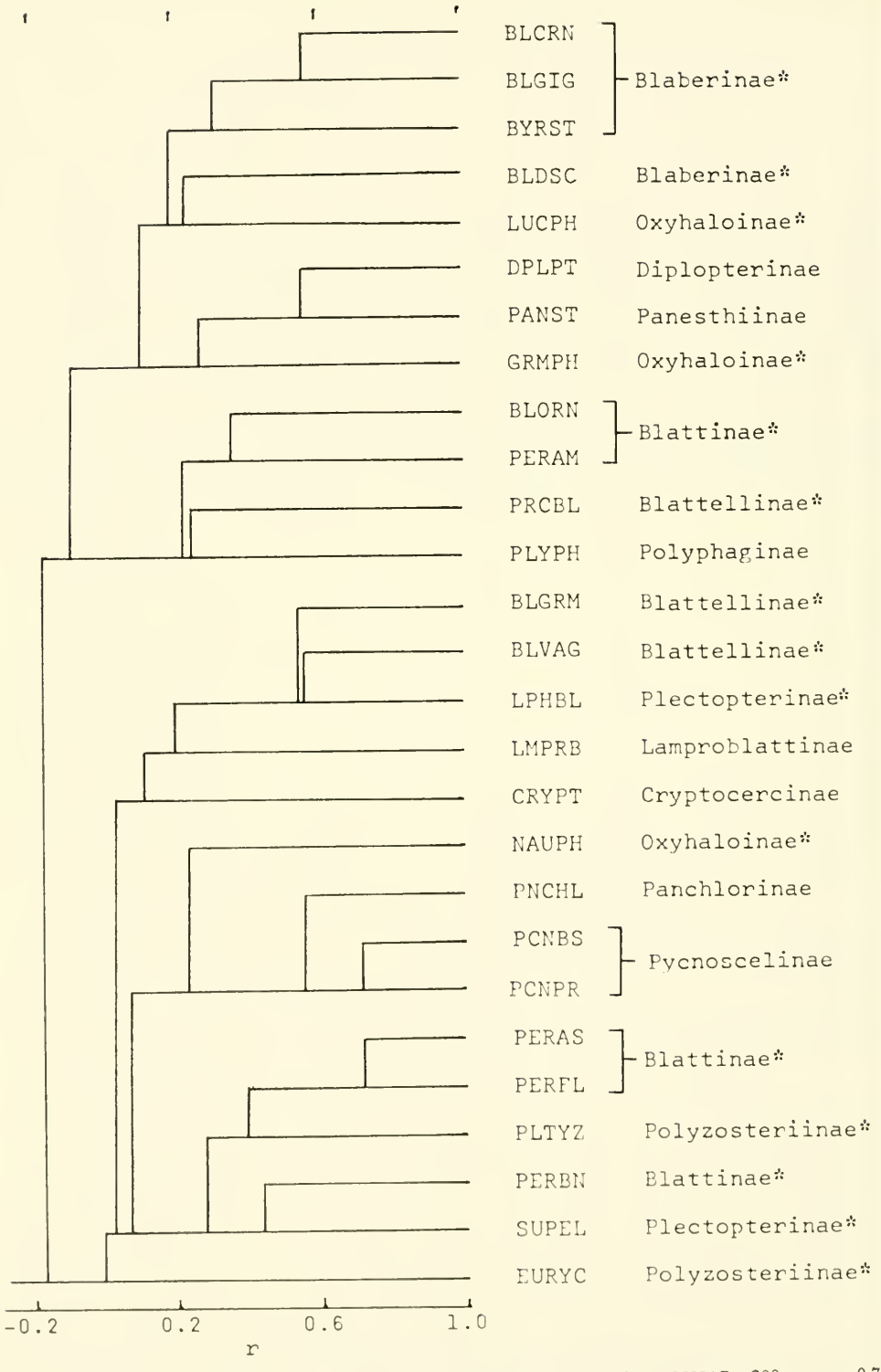


FIG. 32. Phenogram of correlation coefficients among small female nymphs. NCHAR=200. r_{coph}=0.763.

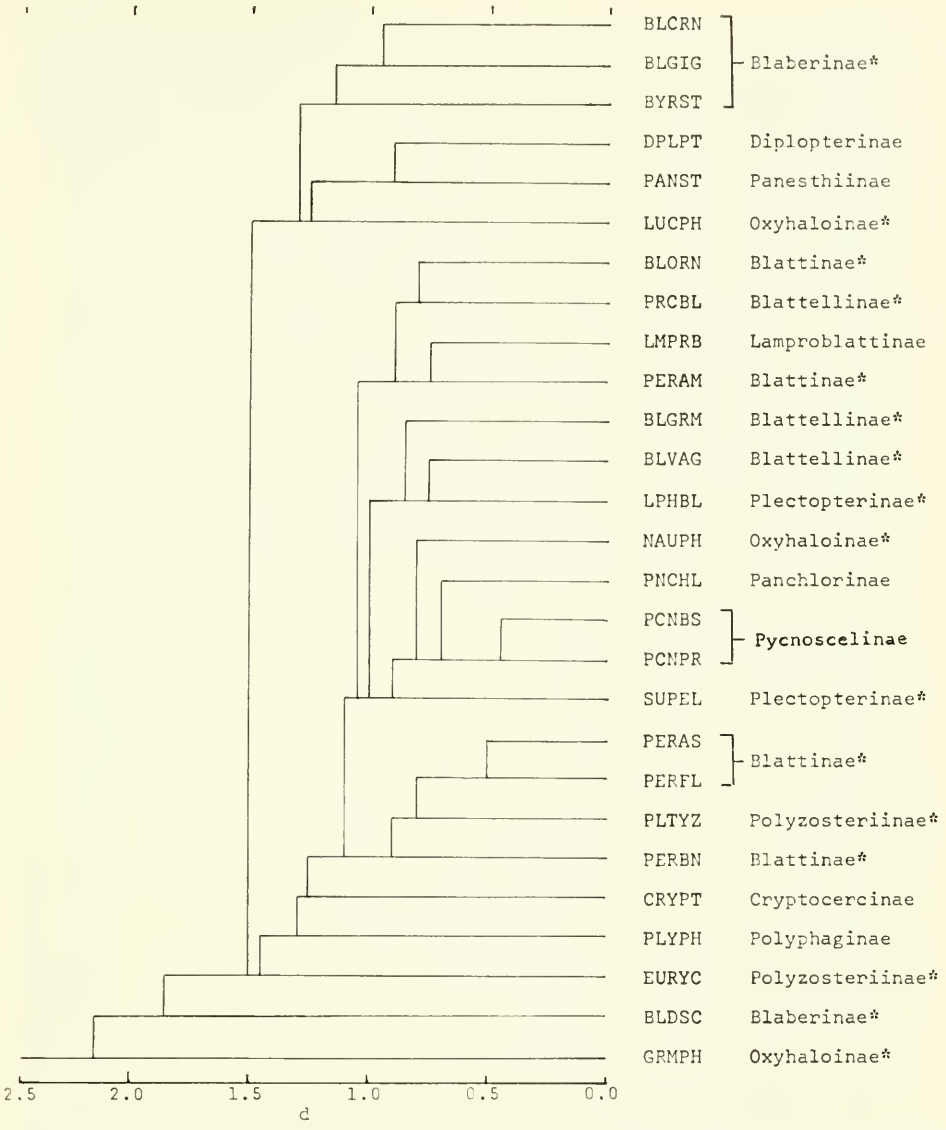
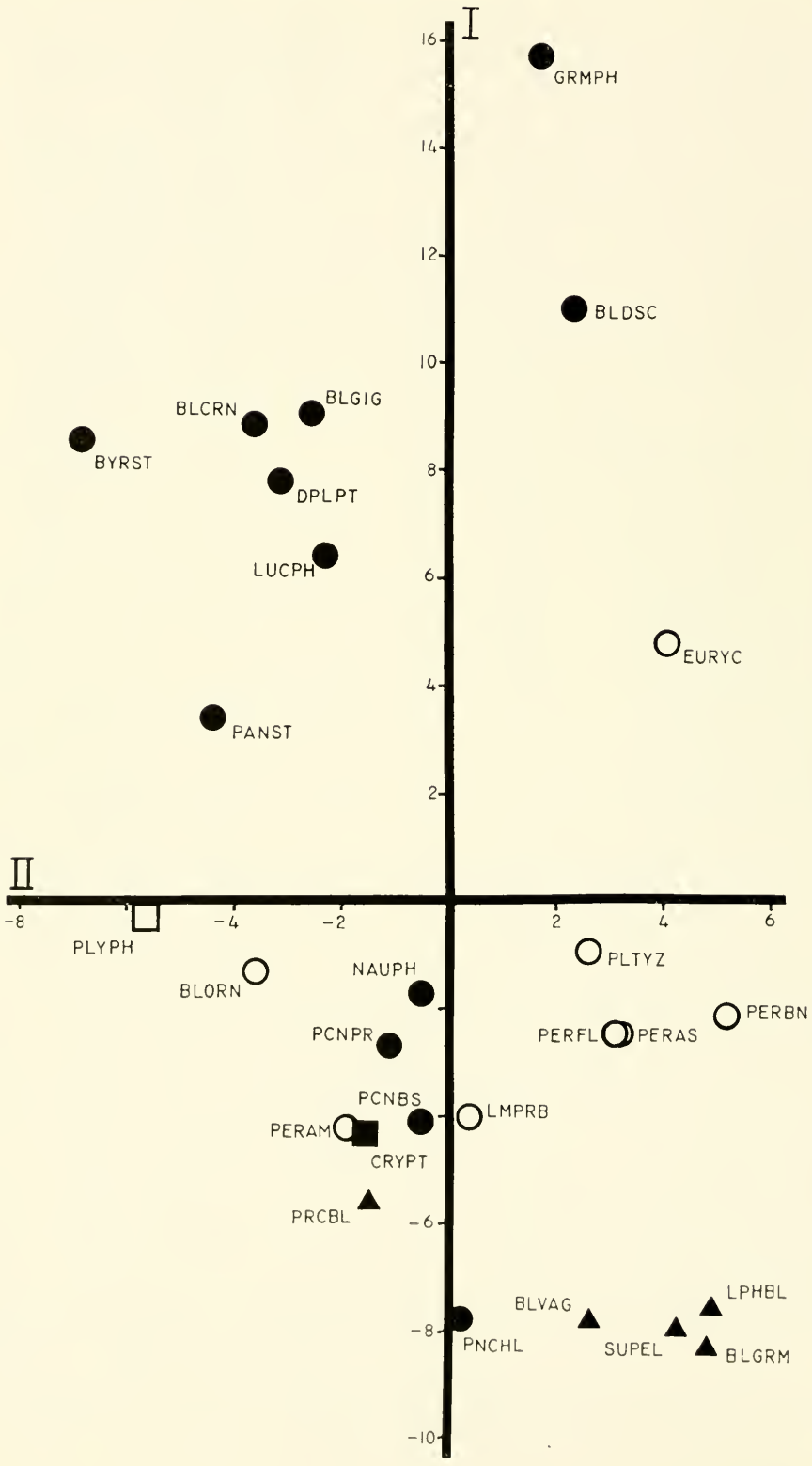


FIG. 33. Phenogram of distance coefficients among small female nymphs. NCHAR=200. r_{coph}=0.912.


I
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16
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-2
-4
-6
-8
-10
-8
-4
-2
2
4
6
GRMPH
BLDSC
BLCRN
BLGIG
BYRST
DPLPT
LUCPH
EURYC
PANST
PLYPH
PLTYZ
BLORN
NAUPH
PERBN
PERFL
PERAS
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PCNBS
LMPRB
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CRYPT
PRCBL
LPHBL
BLVAG
PNCHL
SUPEL
BLGRM

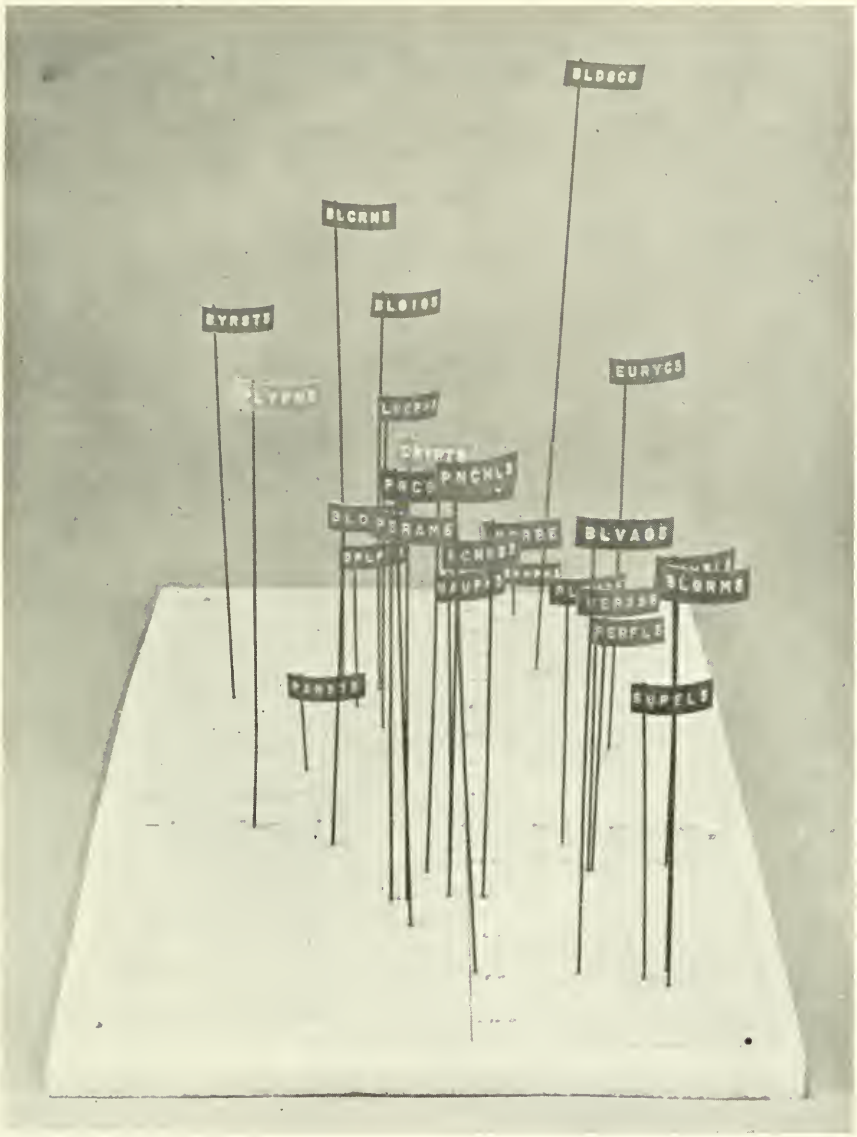


FIG. 34. Centroid component analysis of small female nymphs. Two-dimensional diagram (left) and three-dimensional model (above). "5" identifies a small female nymph. NCHAR=137. r_{coph}=0.863. Factor I=33.1%, II=7.9%, III=8.8% of total variance. Total extracted variance=49.8%.

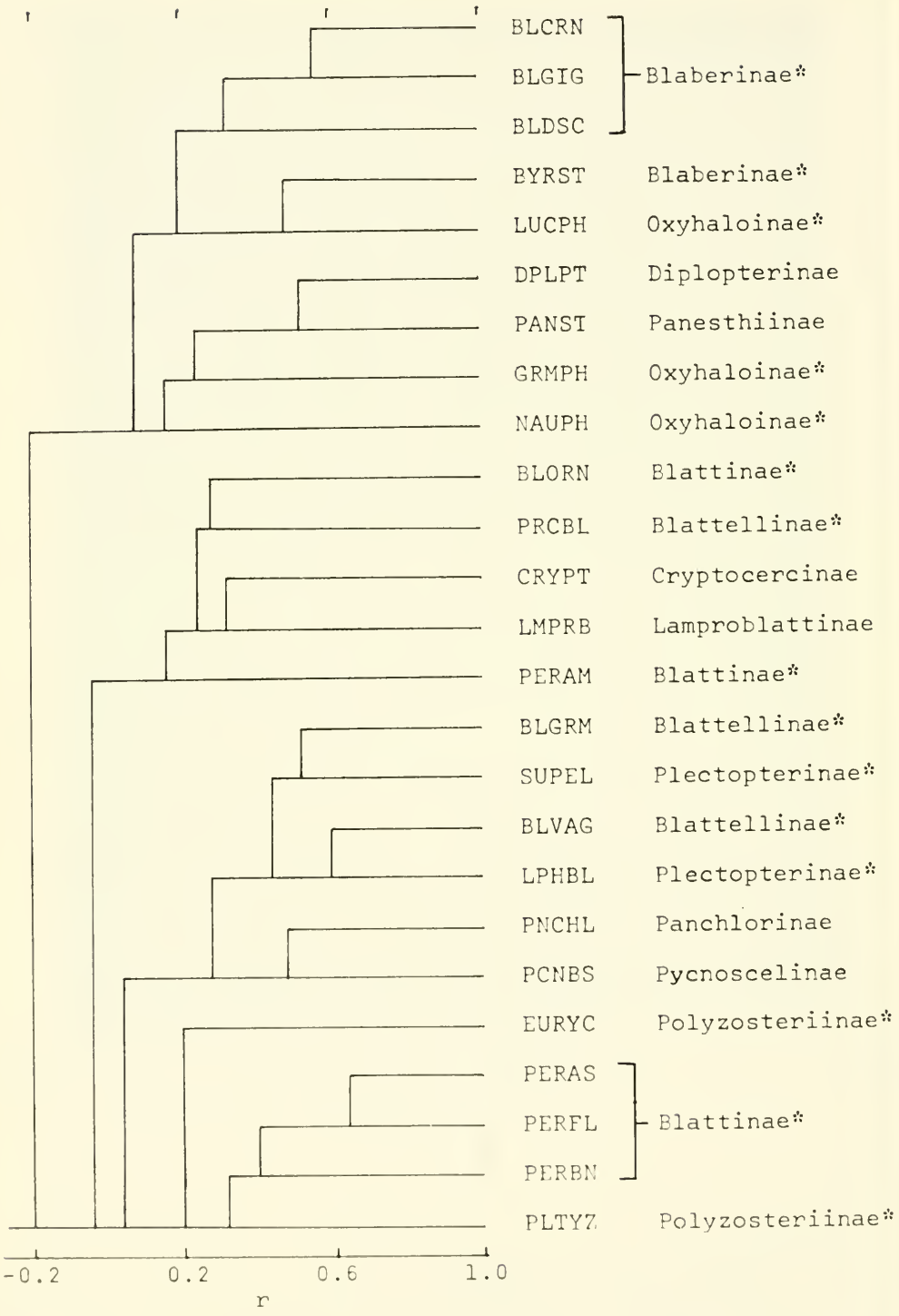


FIG. 35. Phenogram of correlation coefficients among small male nymphs. NCHAR=196. r_{coph}=0.772.

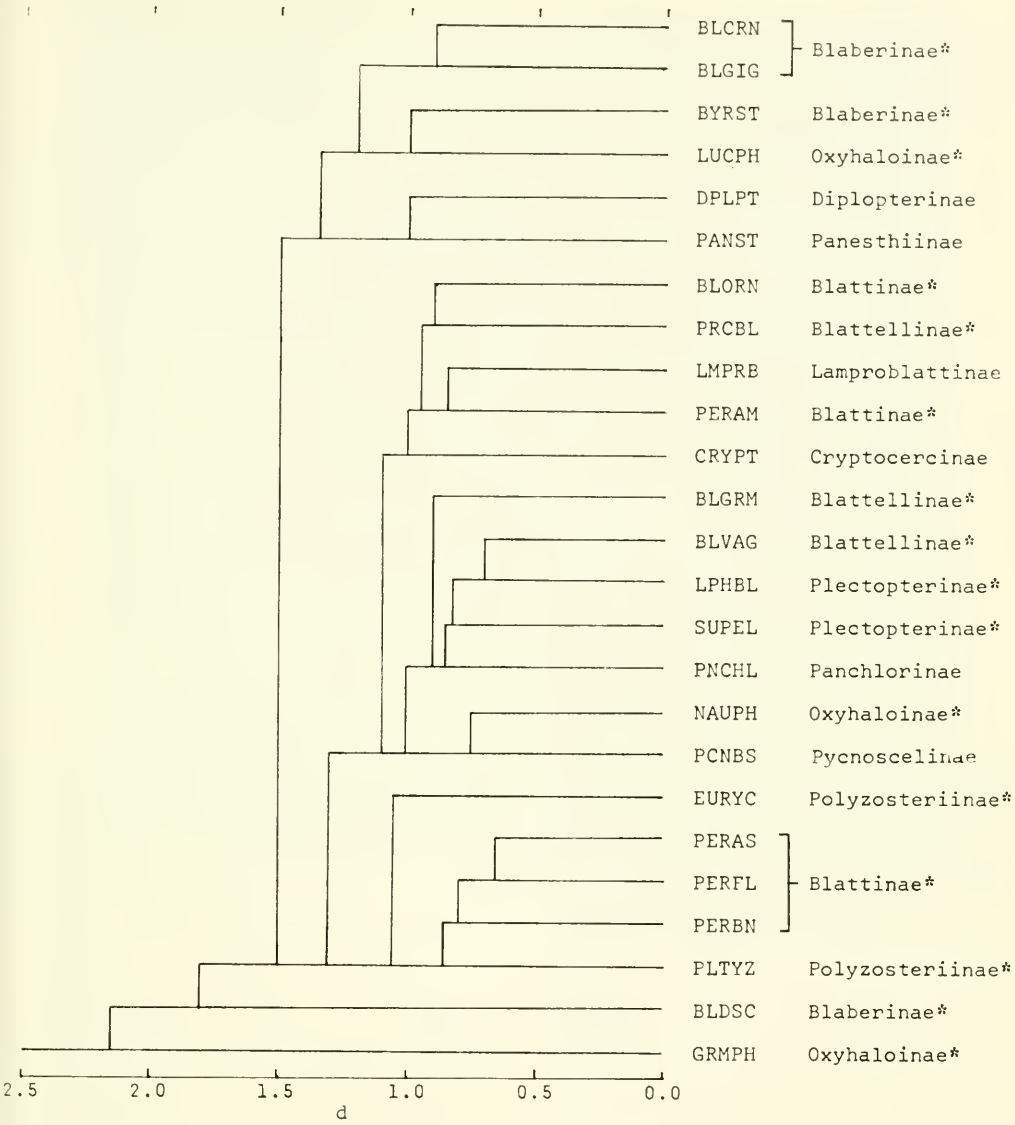
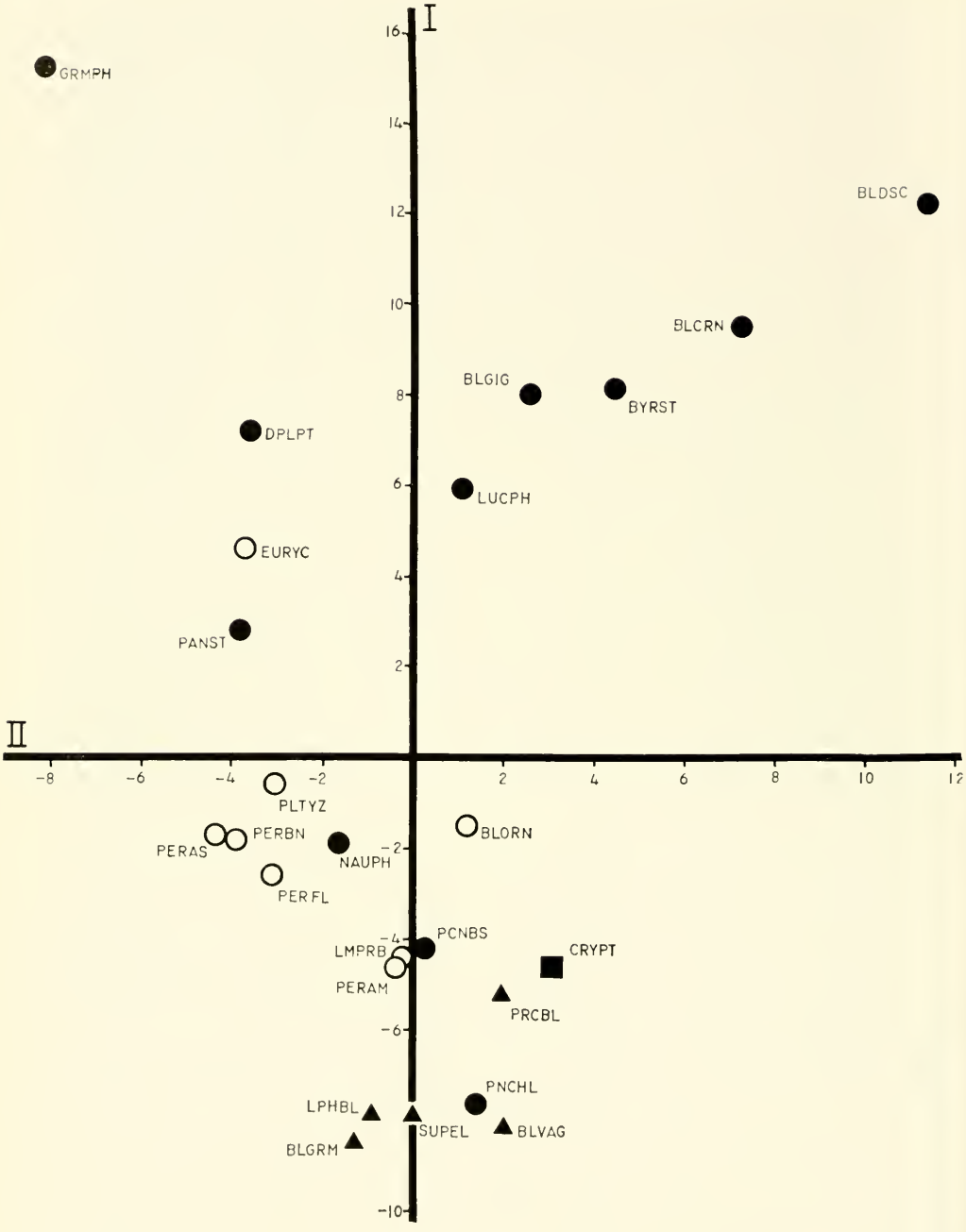


Fig. 36. Phenogram of distance coefficients among small male nymphs. NCHAR=196. r_{coph}=0.887.


I
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-4
-6
-8
-10
-8
-6
-4
-2
2
4
6
8
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GRMPH
BLDSC
BLCRN
BLGIG
BYRST
DPLPT
LUCPH
EURYC
PANST
PLTYZ
PERAS
PERBN
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PERAM
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PNCHL
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BLVAG
BLGRM

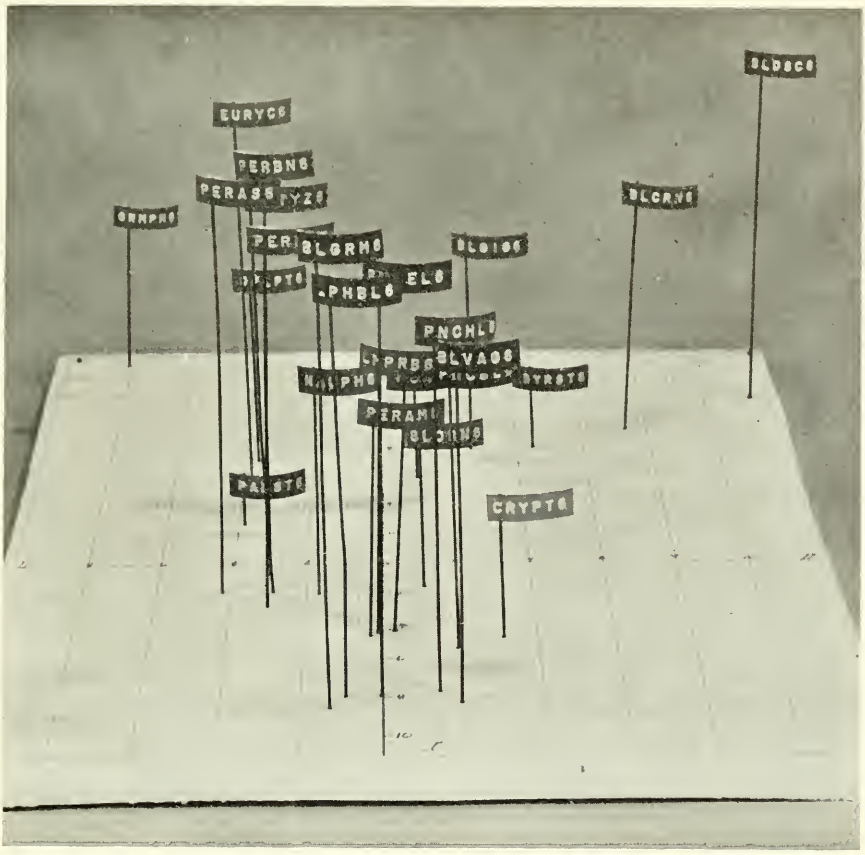


FIG. 37. Centroid component analysis of small male nymphs. Two-dimensional diagram (left) and three-dimensional model (above). "6" identifies a small male nymph. NCHAR=136. r_{coph}=0.802. Factor I=35.7%, II=11.8%, III=6.9% of total variance. Total extracted variance=54.4%.

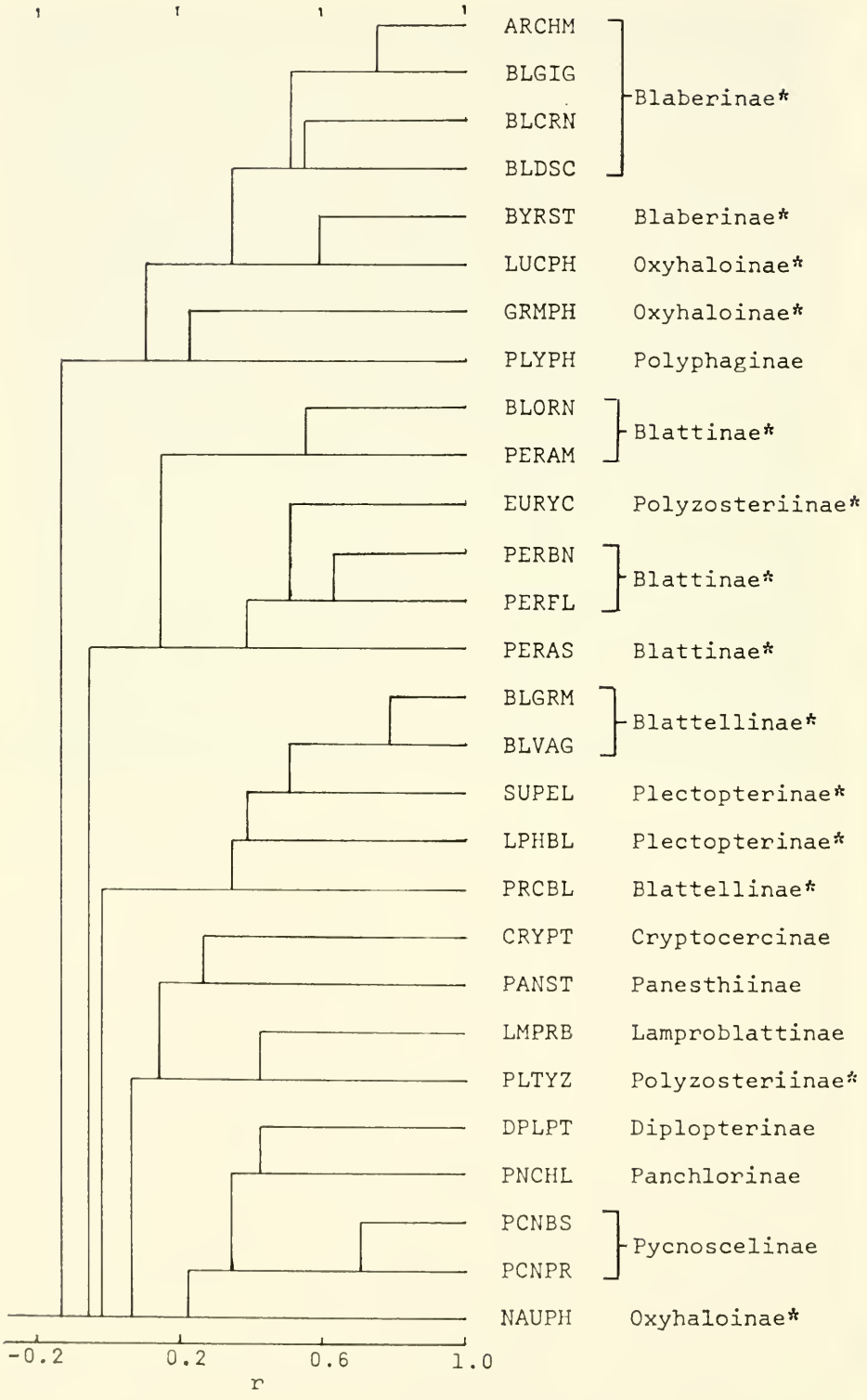


FIG. 38. Phenogram of correlation coefficients among large female nymphs. NCHAR=212. r_{coph}=0.824.

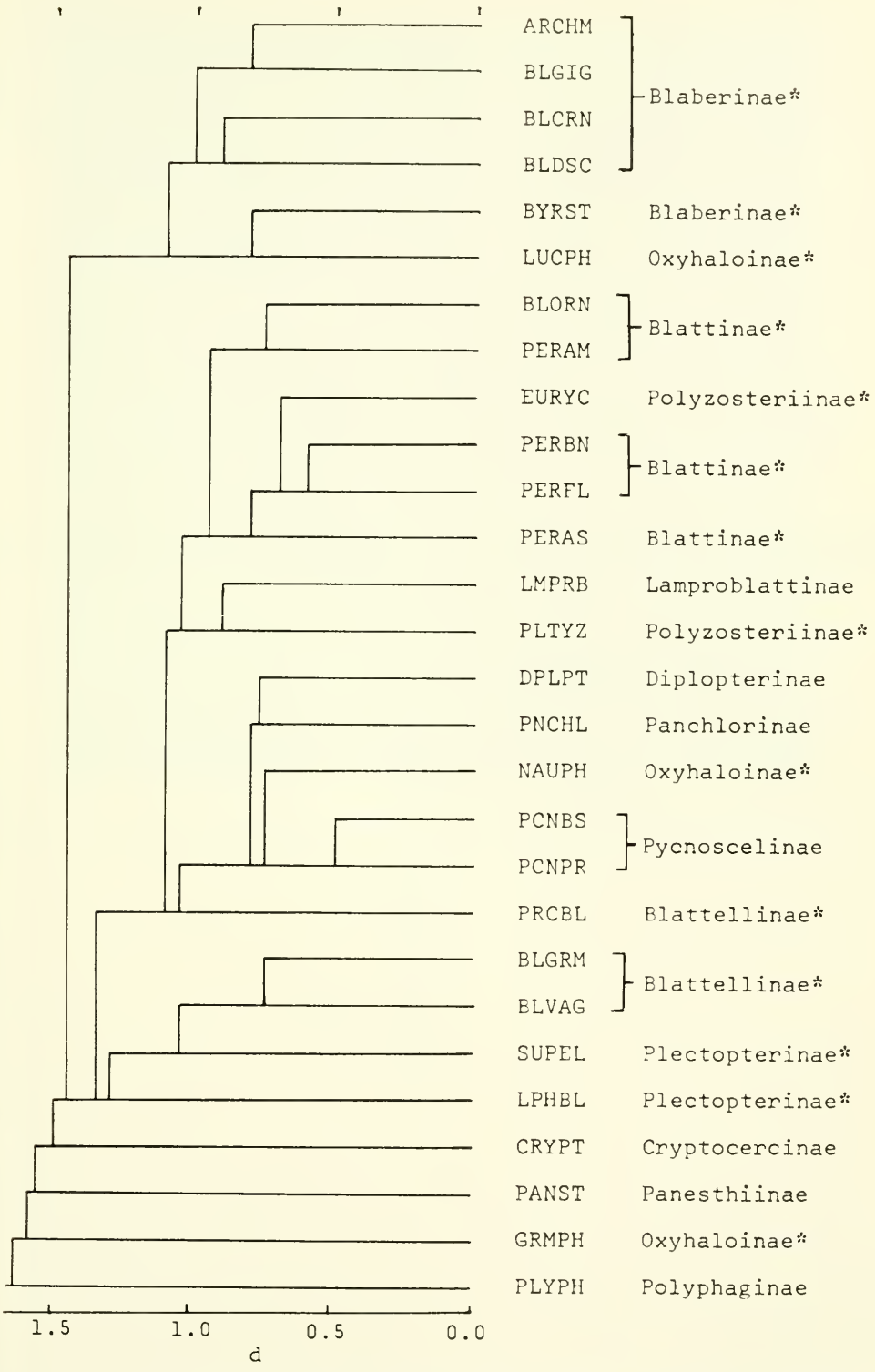
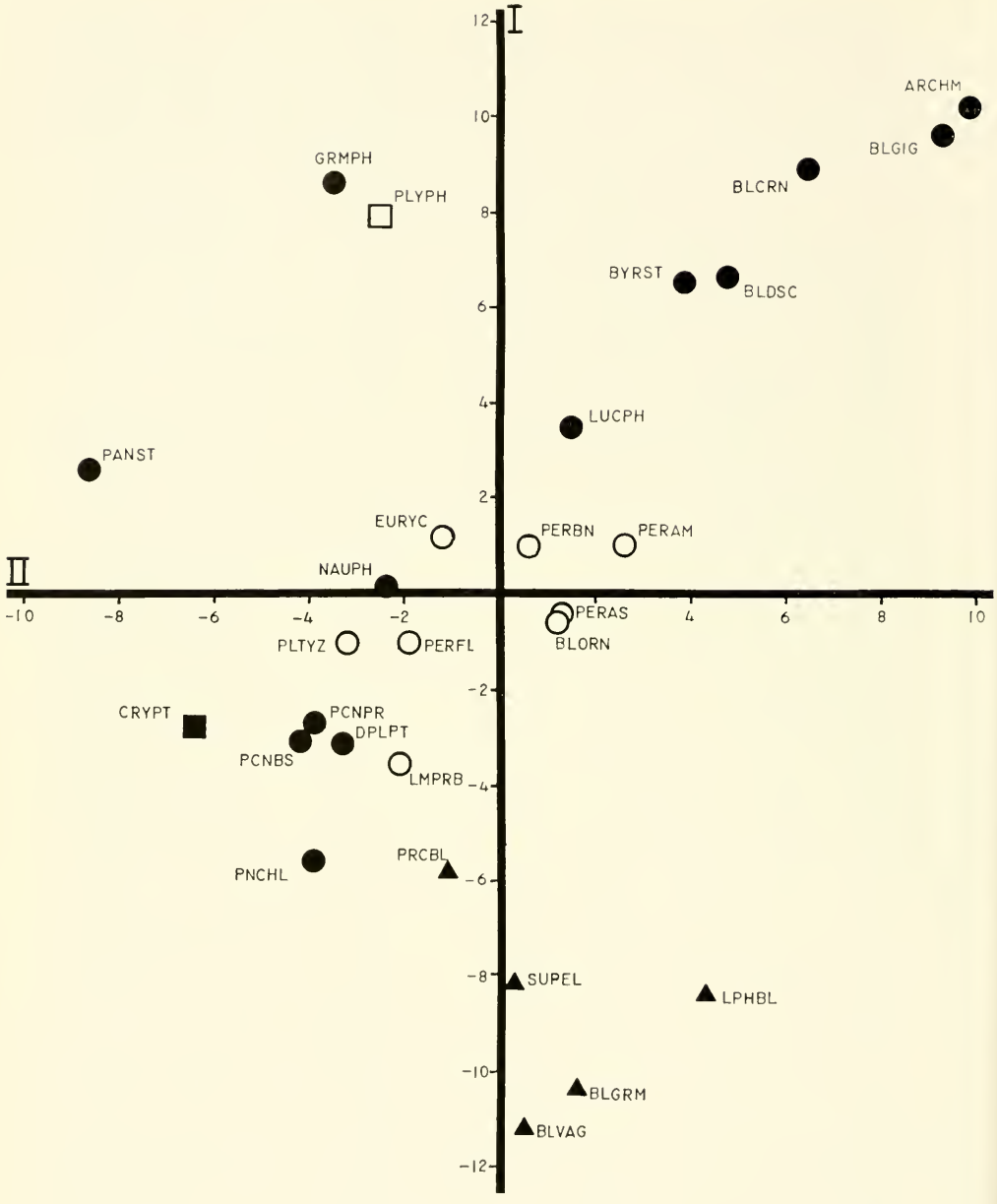


Fig. 39. Phenogram of distance coefficients among large female nymphs. NCHAR=212. r_{coph}=0.818.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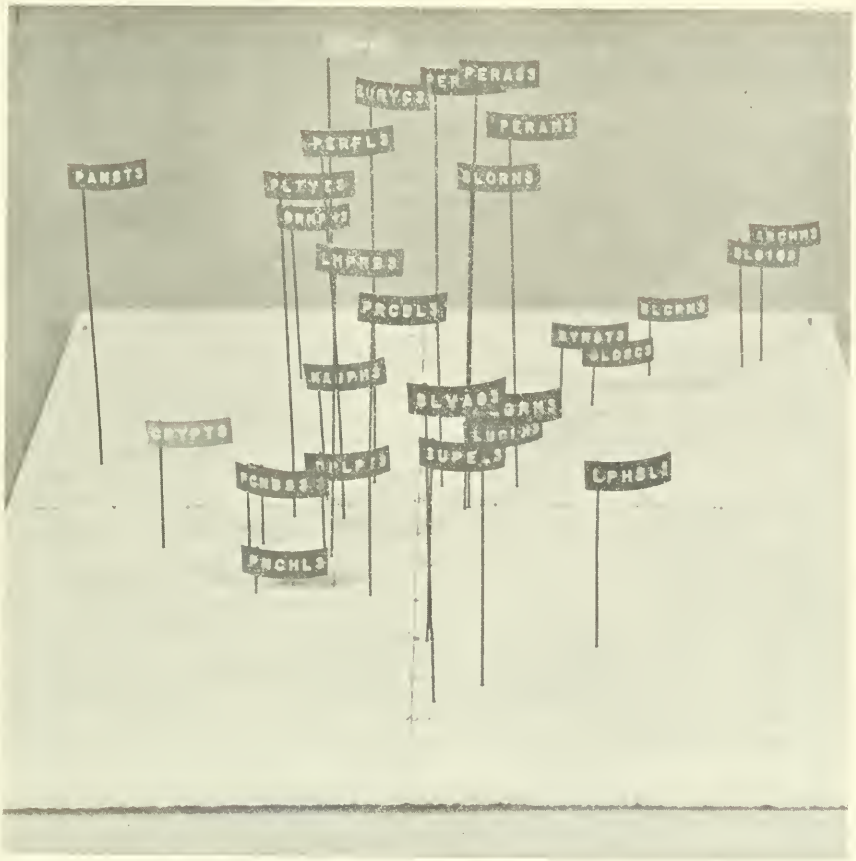


FIG. 40. Centroid component analysis of large female nymphs. Two-dimensional diagram (left) and three-dimensional model (above). "3" identifies a large female nymph. NCHAR=140. r_{coph}=0.805. Factor I=26.0%, II=12.8%, III=8.8% of total variance. Total extracted variance=47.6%.

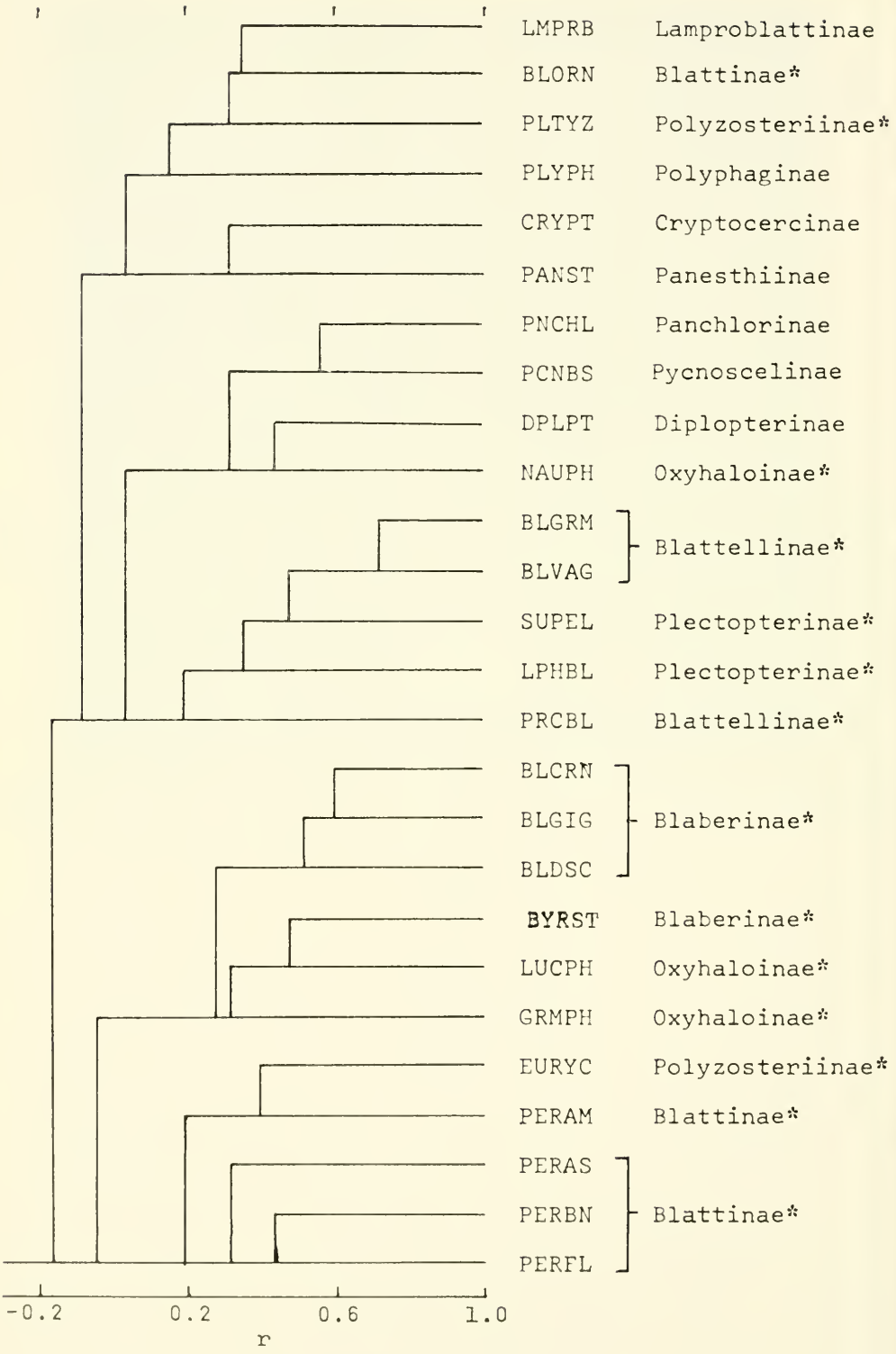


FIG. 41. Phenogram of correlation coefficients among large male nymphs. NCHAR=216. r_{coph}=0.782.

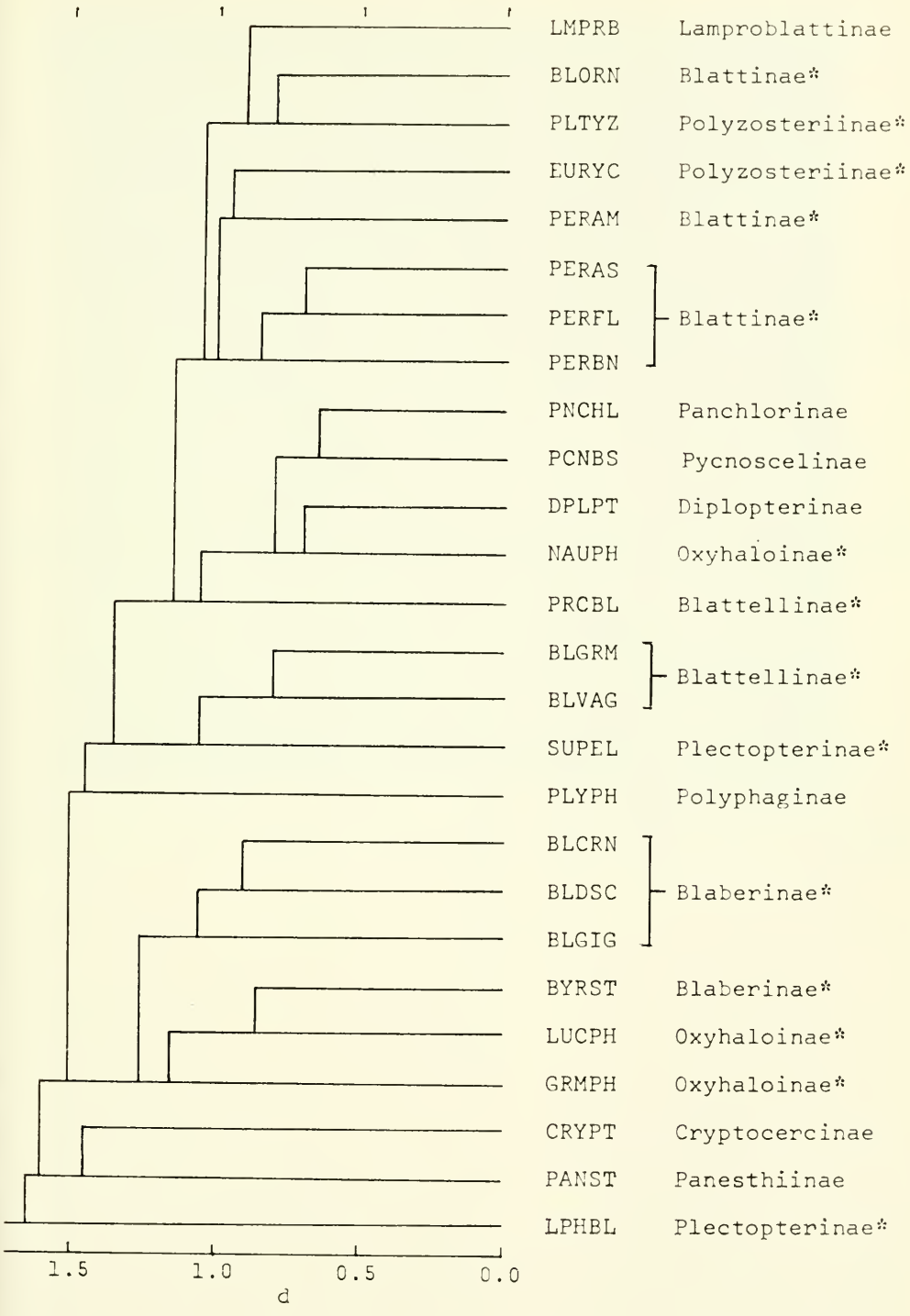
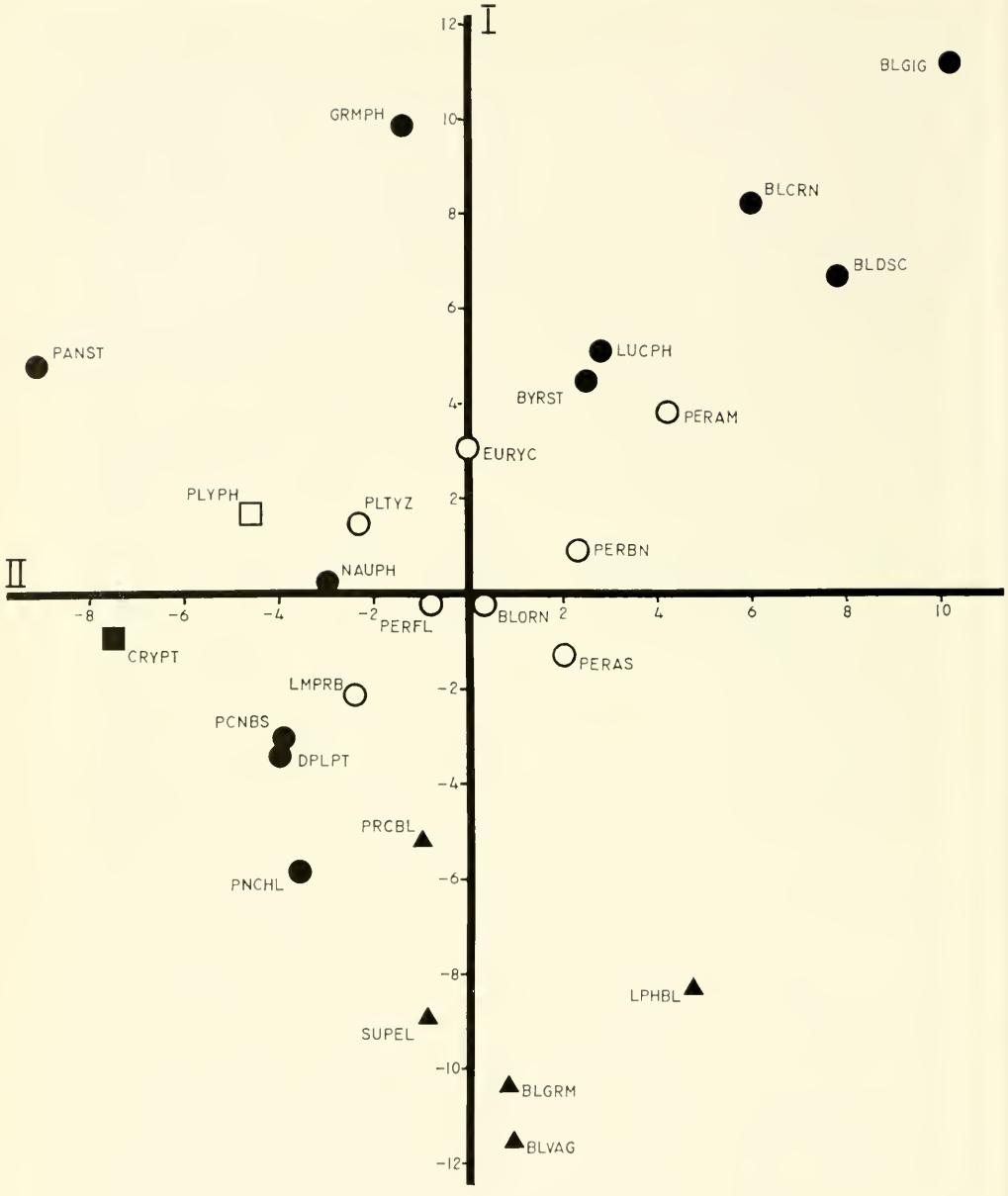


FIG. 42. Phenogram of distance coefficients among large male nymphs. NCHAR=216. r_{coph}=0.742.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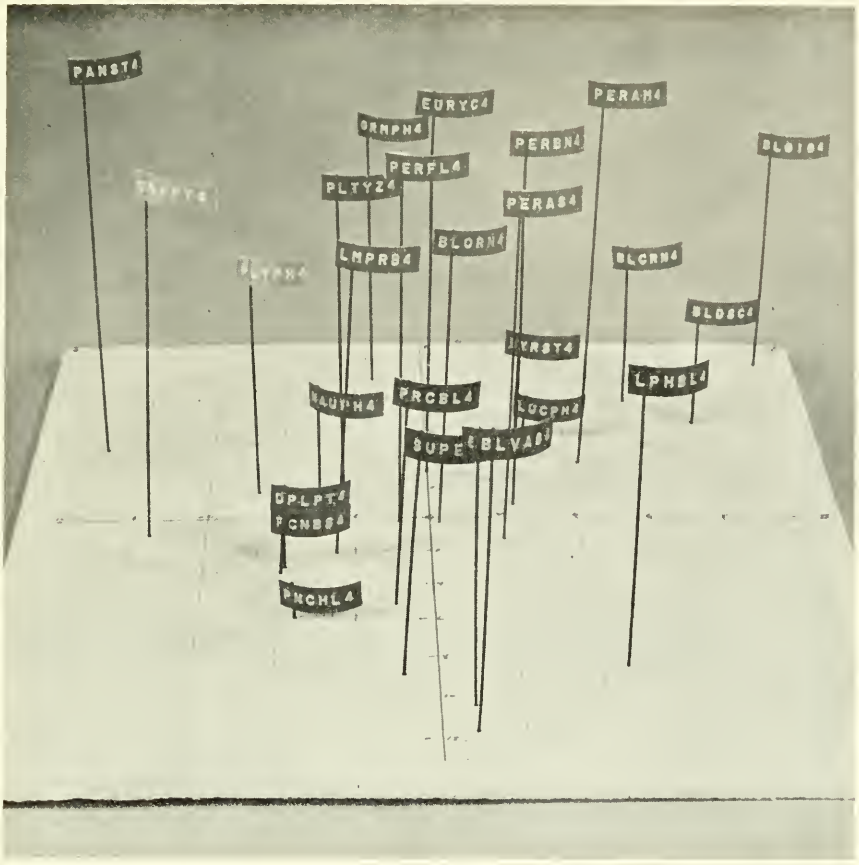
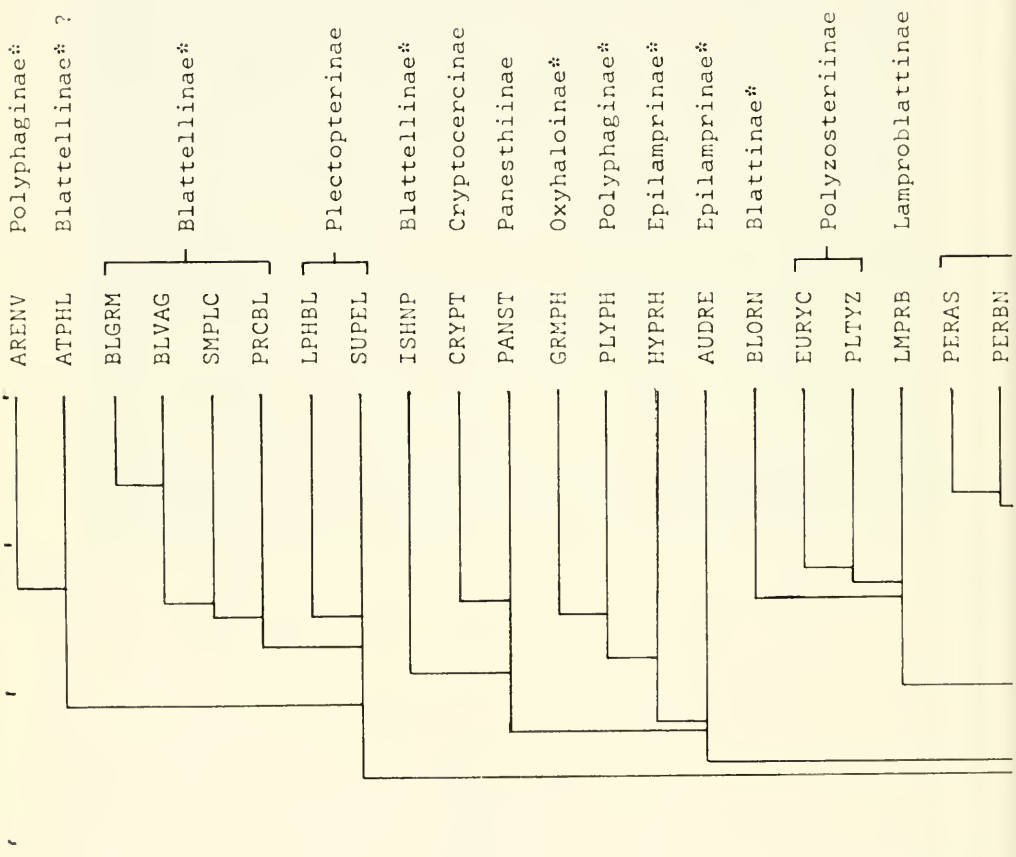


Fig. 43. Centroid component analysis of large male nymphs. Two-dimensional diagram (left) and three-dimensional model (above). "4" identifies a large male nymph. NCHAR=146. r_{coph}=0.714. Factor I=24.5%, II=13.1%, III=7.1% of total variance. Total extracted variance=44.7%.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Polyphaginae*
Blattellinae* ?
Blattellinae*
Plectopterinae
Blattellinae*
Cryptocercinae
Panesthiinae
Oxyhaloinae*
Polyphaginae*
Epilamprinae*
Epilamprinae*
Blattinae*
Polyzosteriinae
Lamproblattinae

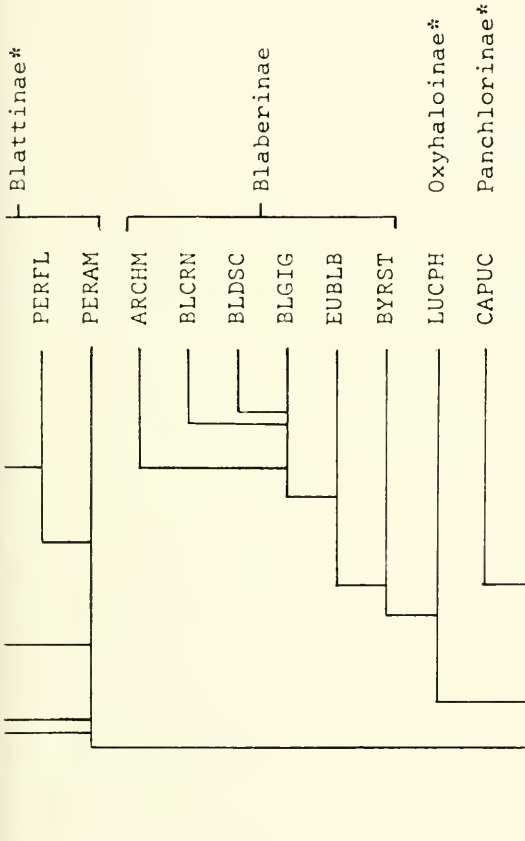
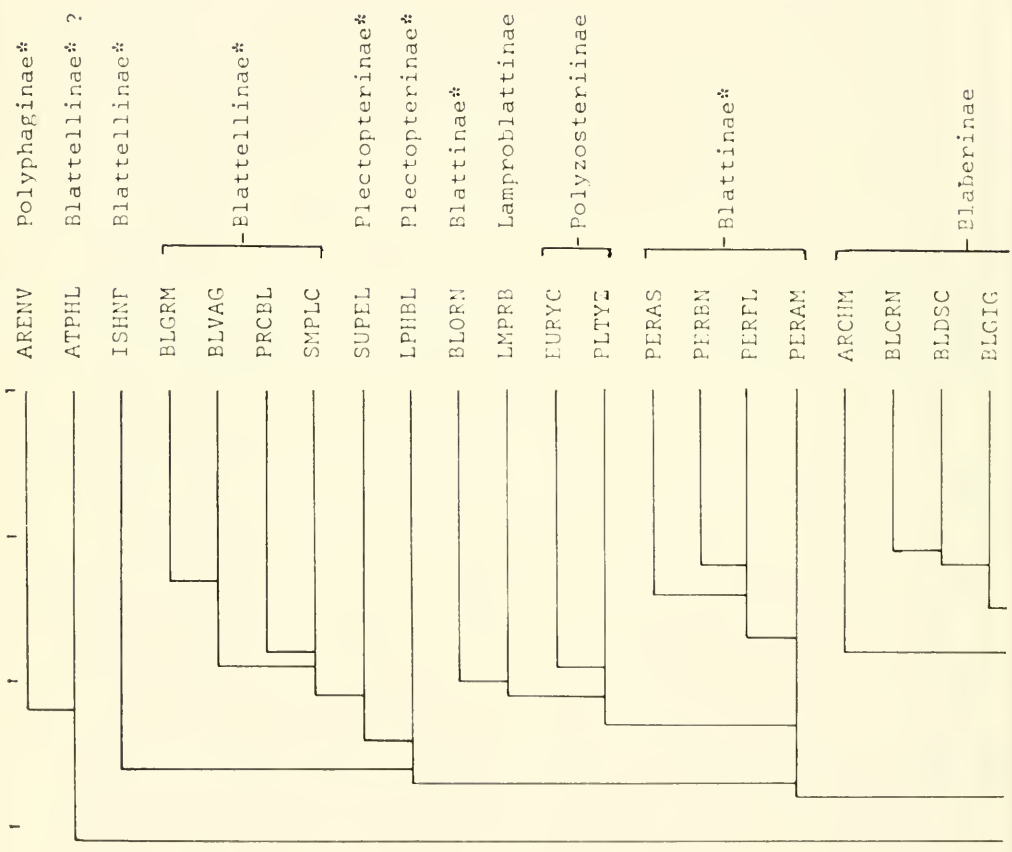


Fig. 44. Phenogram of correlation coefficients among female adults. NCHAR=335. r_{coph}=0.787.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Plectopterinae*
Plectopterinae*
Blattinae*
Lamproblattinae
Polyzosterilinae
Blattinae*
Blaberinae

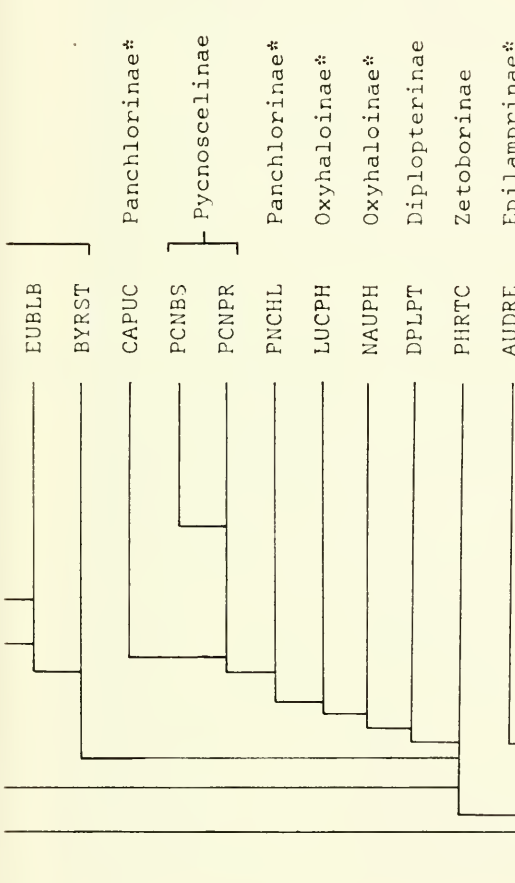
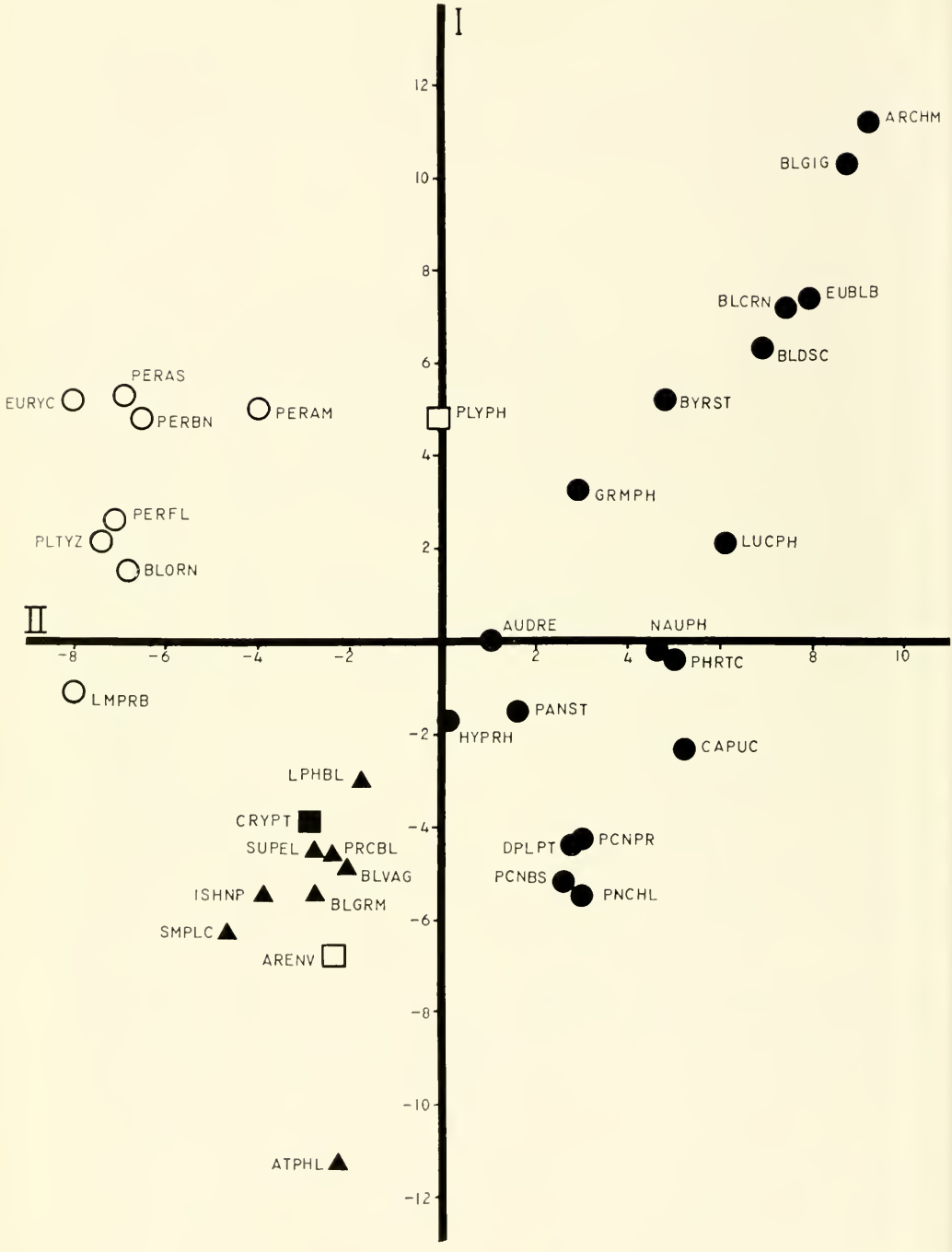


Fig. 45. Phenogram of distance coefficients among female adults. NCHAR=335. r_{coph}=0.742.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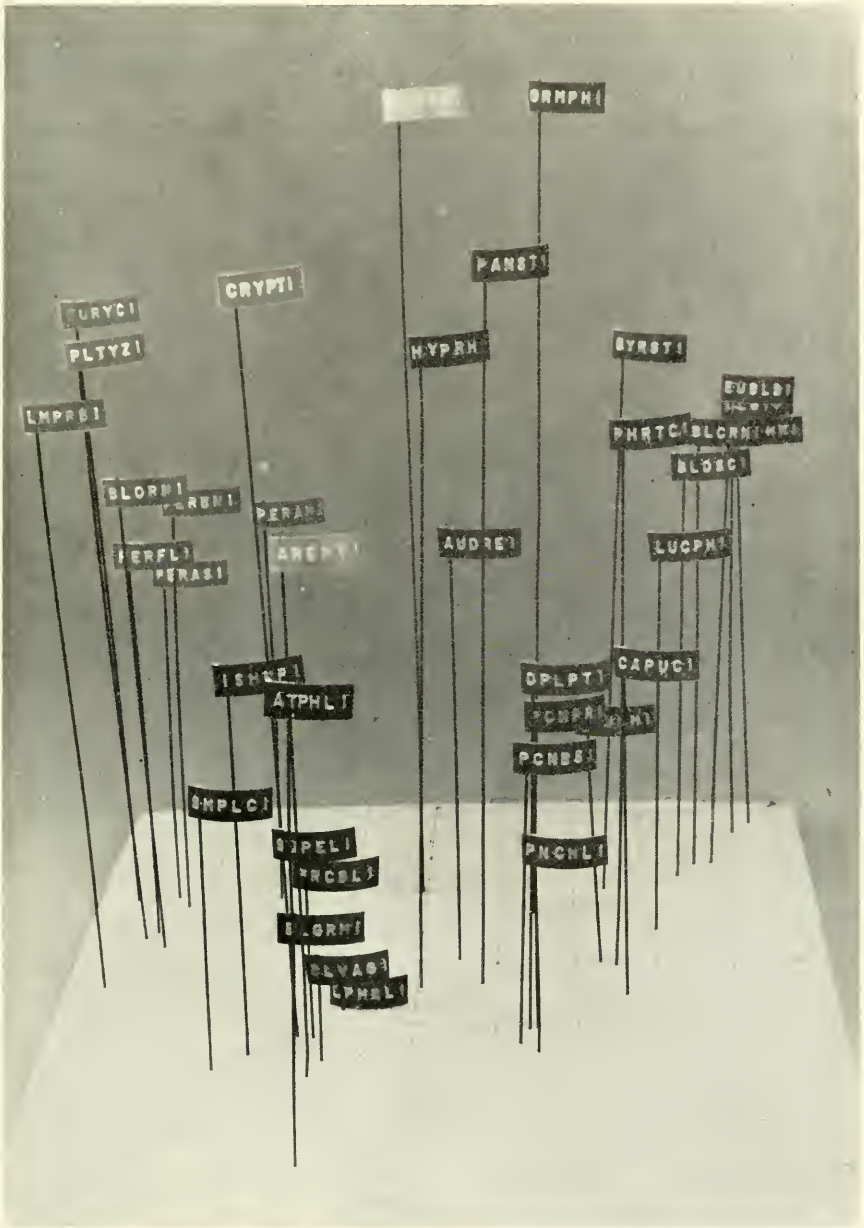
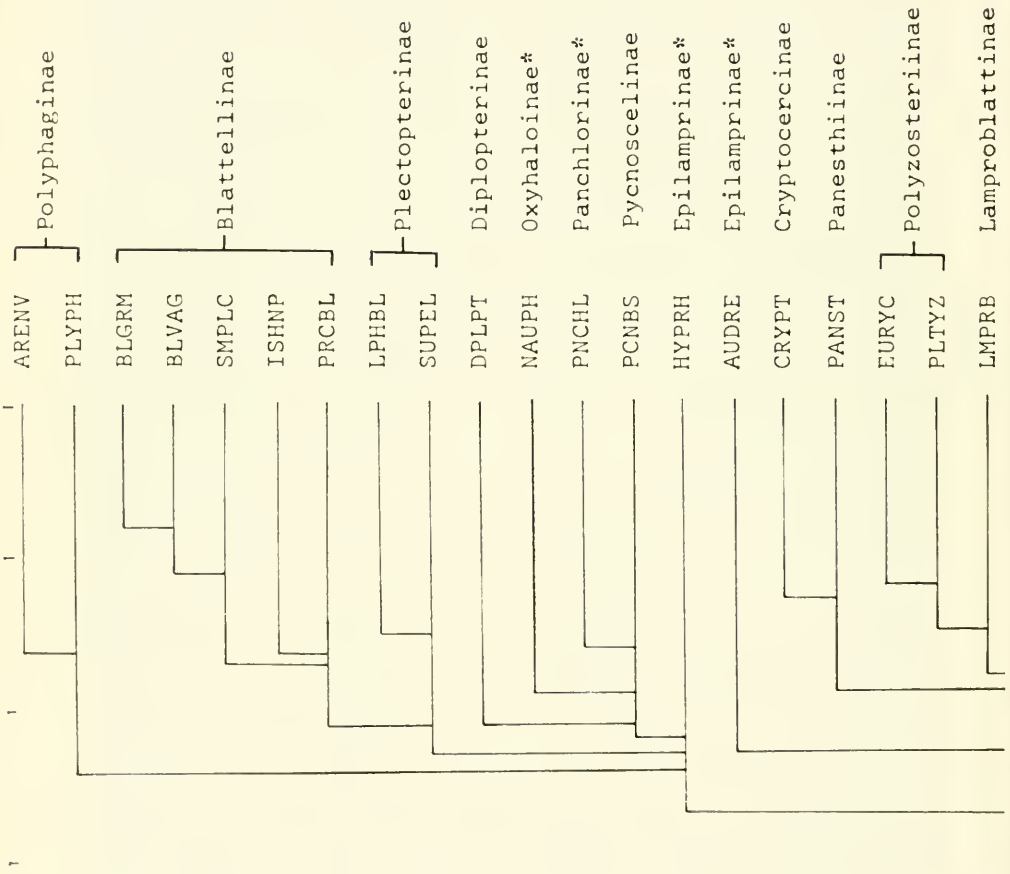


FIG. 46. Centroid component analysis of female adults. Two-dimensional diagram (left) and three-dimensional model (above). "1" identifies a female adult. NCHAR=168. r_{coph}=0.760. Factor I=15.9%, II=15.5%, III=13.2% of total variance. Total extracted variance=44.6%.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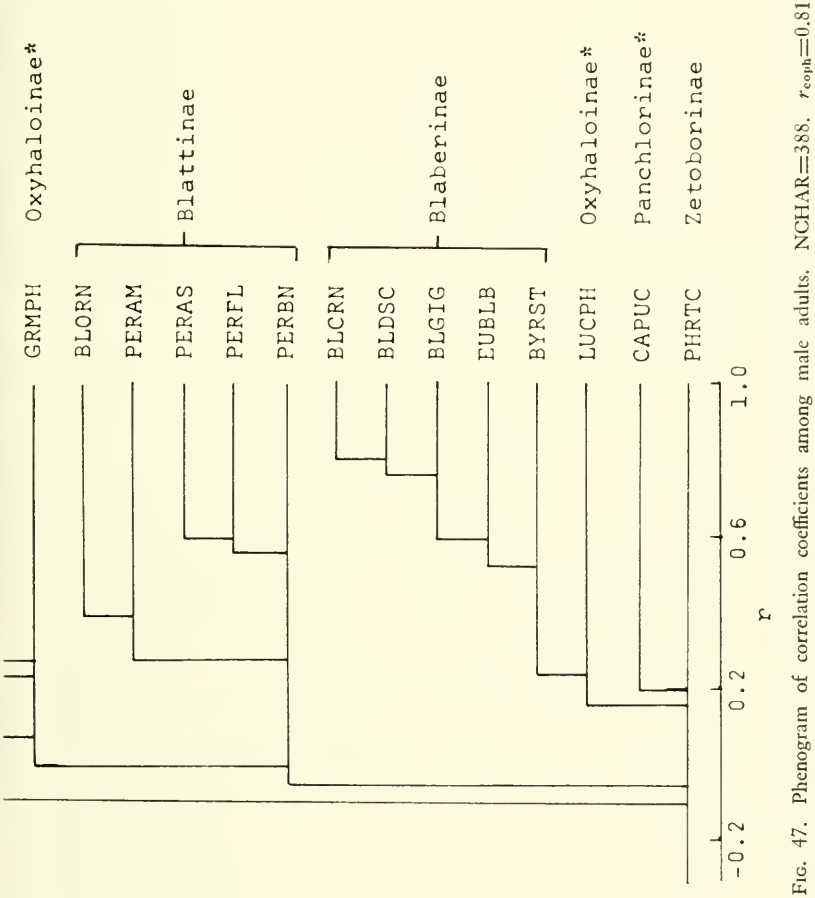
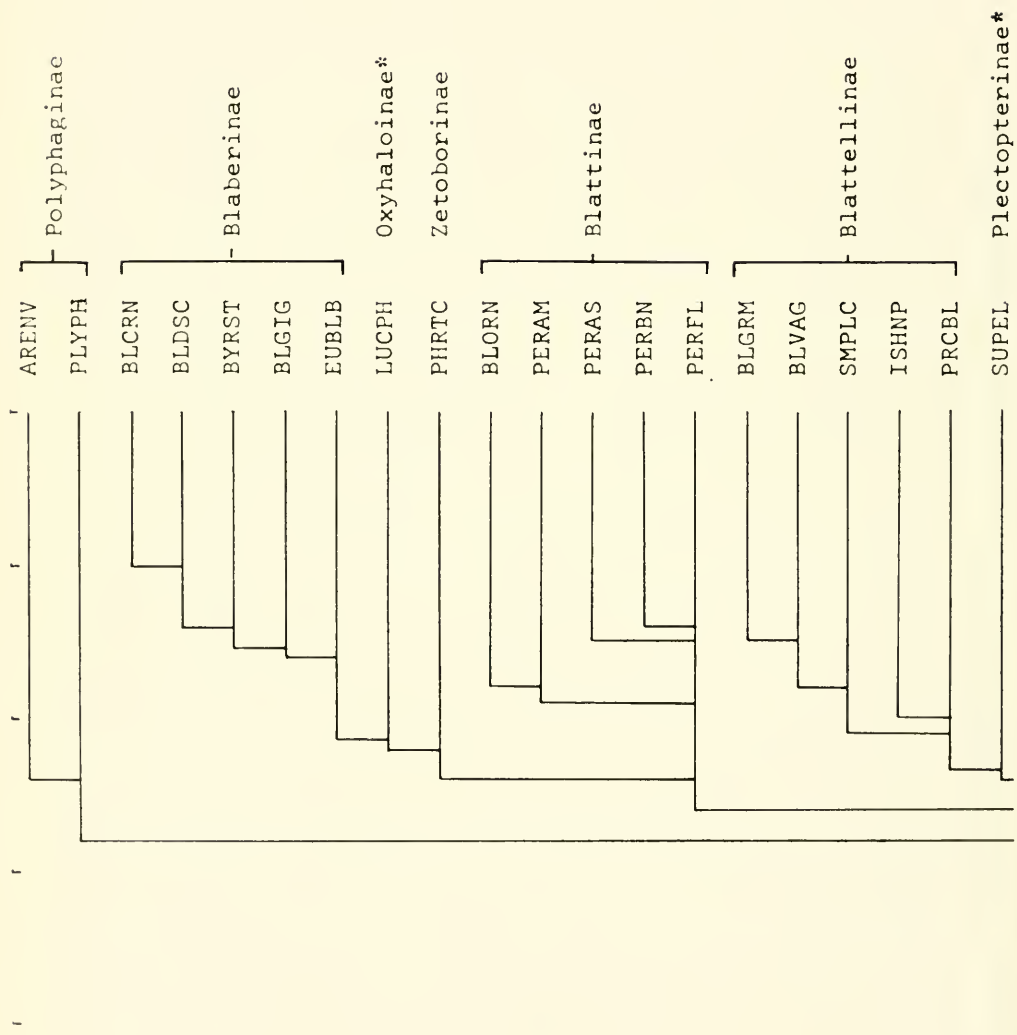


Fig. 47. Phenogram of correlation coefficients among male adults. NCHAR=388. r_{coph}=0.817.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Zetoborinae
BLORN
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SUPEL
Plectopterinae*

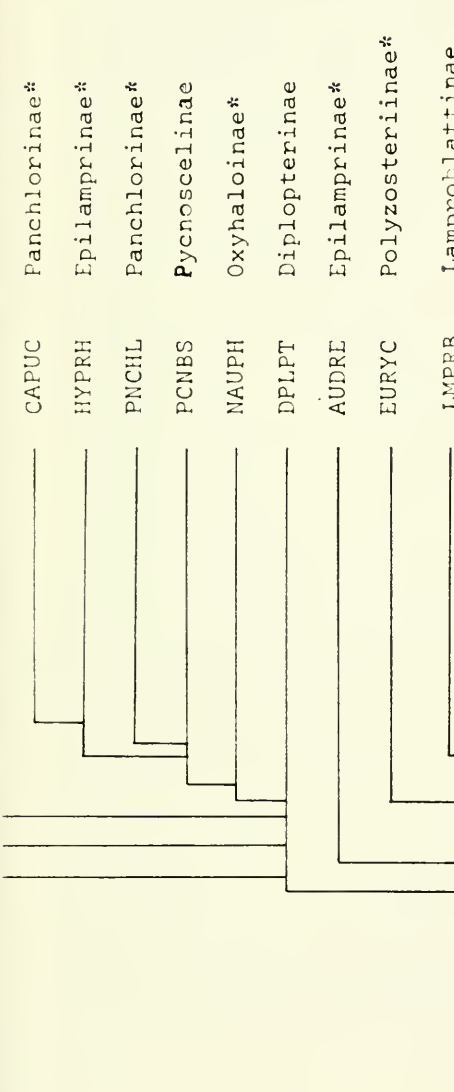
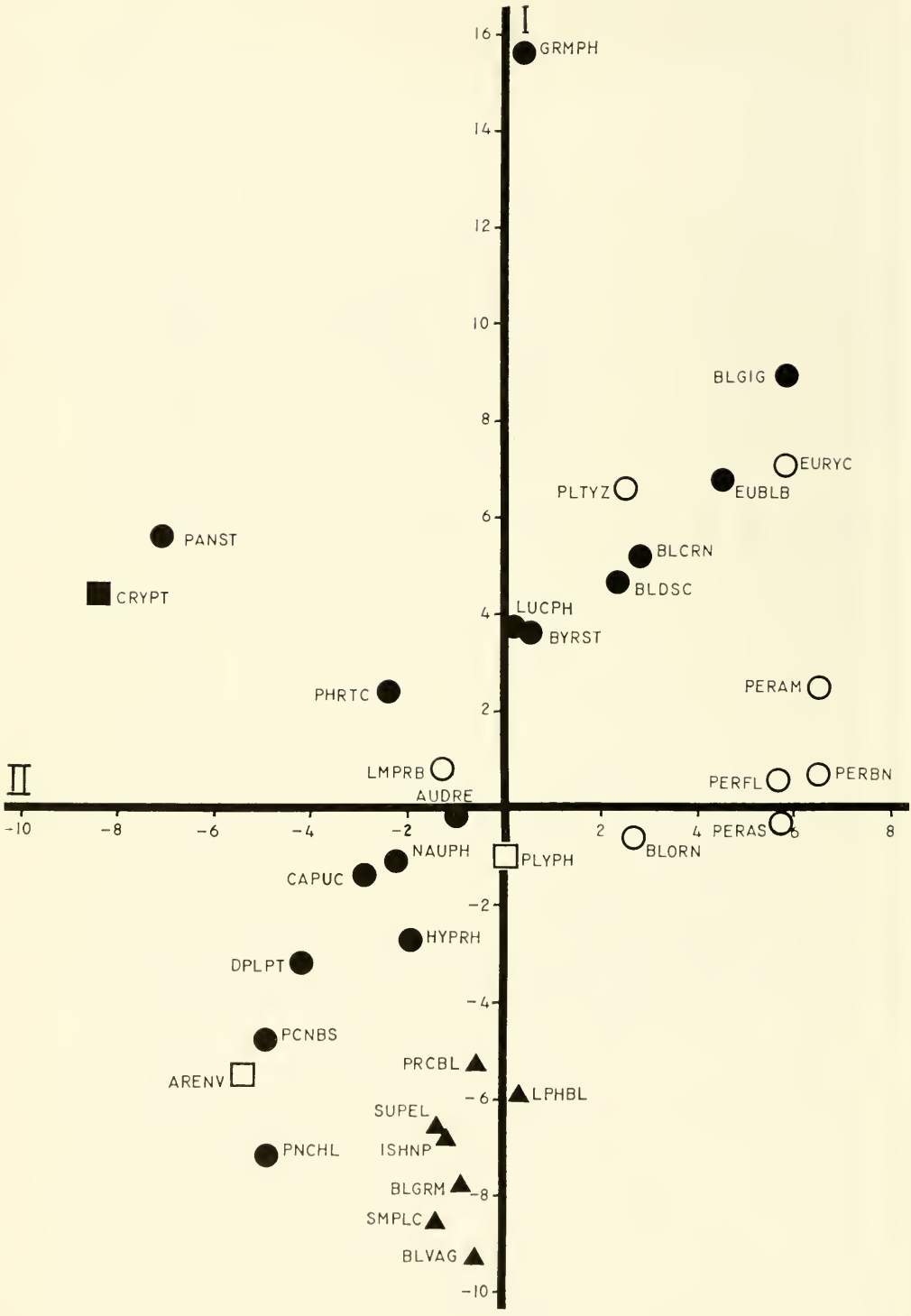


FIG. 48. Phenogram of distance coefficients among male adults. NCHAR =388. r_{coph}=0.814.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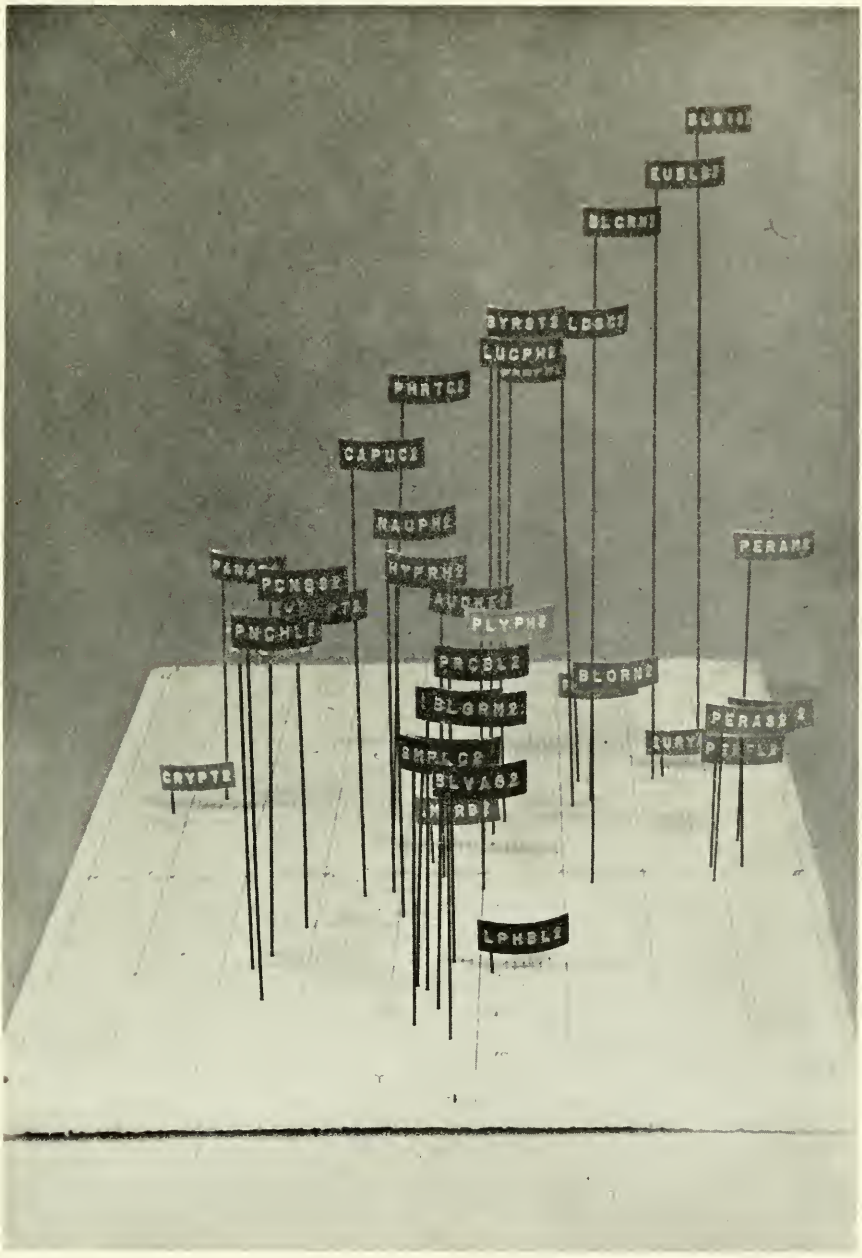

FIG. 49. Centroid component analysis of male adults. Two-dimensional diagram (left) and three-dimensional model (above). "2" identifies a male adult. NCHAR=152. r_{coph}=0.760. Factor I=21.1%, II=9.4%, III=12.2% of total variance. Total extracted variance=42.8%.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

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THE CAECILIANS OF ECUADOR

By

EDWARD H. TAYLOR AND JAMES A. PETERS

Vol. 50, No. 7, pp. 333-346 June 28, 1974

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SCIENCE BULLETIN

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The Caecilians of Ecuador

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The Caecilians of Ecuador

Edward H. Taylor* and James A. Peters**

ABSTRACT

This paper deals with a study of a caecilian collection made in Ecuador largely by the junior author and for the most part not available to the senior author in the preparation of his 1968 monograph on the caecilians.

INTRODUCTION

The junior author spent considerable time in Ecuador collecting in various parts of the country and in studying the collections that have been largely acquired by the United States National Museum. The senior author visited some weeks in the country, all of which time was spent in the field. Both were surprised at the large number of species of caecilians that are to be found there and doubt that so large a number occur in any other area of equal size. We believe that the high continental divide is responsible for dividing the species largely into two groups, one occurring in the Pacific and western Caribbean drainage, the other largely if not entirely in the Atlantic and the eastern Caribbean drainage.

It is true that certain species have been reported in both areas; some of these are in obvious error. Of course it is entirely probable that certain ones do occur in both areas.

The senior author believes that the Linnaean name *Caecilia tentaculata* was originally applied to a now unidentifiable species (the type now lost). The matter is being investigated.

The following museum abbreviations are used:

BMNH: British Museum of Natural History, London.

EPN: Escuela Politechnica Nacional Ecuador, Quito.

JAP: James A. Peters, Private Collection, Washington, D.C.

KUMNH: Kansas University Museum of Natural History, Lawrence, Kansas.

USNM: United States National Museum, Washington, D.C.

SPECIES ACCOUNTS

Family **Ichthyophiidae**

Of the two South American genera, *Rhinatrema* and *Epicrionops,* recognized in the family Ichthyophiidae, only the latter is known to occur in Ecuador. One of the most striking characters separating these genera is that *Rhinatrema* has a transverse anal vent, *Epicrionops* a longitudinal vent. There is also a striking difference in the character of the caudal appendage of the two forms.

Epicrionops appears to be distributed from Perú north and east as far as eastern Venezuela, while *Rhinatrema* is known only from the type-locality in Cayenne. Three forms of *Epicrionops* are recognized in Ecuador. These are *E. bicolor, E. marmoratus,* and *E. petersi petersi.*

Epicrionops bicolor Boulenger

Epicrionops bicolor Boulenger, Ann. Mag. Nat. Hist., ser. 5, vol. 11, 1883, pp. 202-203 (type-locality, "Intac, 3900 ft. elevation in western Ecuador").

The type was collected in Ecuador. Presumably the species is confined to the Pacific drainage area. The type is redescribed by Taylor (1968).

* Research Associate, Kansas University Museum of Natural History, Lawrence, Kansas.

** Curator, Division of Reptiles and Amphibians, U.S. National Museum, Washington, D.C. Deceased, December, 1972.

The junior author and Robert Copping collected a specimen of this genus, JAP 4092, on May 9, 1959, on the cacao farm of Colonel Dyott, at kilometer 121 from Quito, six kilometers east of Santo Domingo de los Colorados, Pichincha Province, Ecuador, at an altitude of about 675 meters. The specimen was found in a thoroughly rotted, termite riddled log lying partly in a small stream in a brush-choked ravine. The area is one of fairly heavy rain forest. The light areas of this individual were bright yellow; the dark areas were coffee brown. Unfortunately, the specimen cannot currently be located, but a series of color photographs of it is available.

The species to which it probably belongs is *E. bicolor,* since there seems to be no sign of the marbling characteristic of *E. marmoratus.* We hesitate to assign it to *bicolor,* however, since the specimen is not available, and the locality from whence it comes is almost the same as that for all known specimens of *marmoratus.*

Epicrionops marmoratus Taylor

Epicrionops marmoratus Taylor, The Caecilians of the World, 1968, pp. 205-209, figs. 98-101 (type-locality, Santo Domingo de los Colorados, Pichincha Province, Ecuador).

The holotype and two paratypes are known. According to the notes of the junior author, made while he was a Fulbright Professor in residence in Quito, Ecuador, the specimen EPN 3986 was collected on the road to Mindo, Pichincha Province, a locality somewhat more precise than that available to the senior author at the time of publication of his monograph. Mindo is on the western Andean slopes at about 1400 meters, while the type-locality lies below it at about 670 meters.

Epicrionops petersi petersi Taylor

Epicrionops petersi petersi Taylor, The Caecilians of the World, 1968, pp. 224-230, figs. 112-116 (type-locality, Agua Rica between Limón and Gualaceo, 6200 ft. [1908 m]).

This species and *Caecilia orientalis* were found together, living under precisely the same environmental conditions. Most of the specimens in the type series were taken under a thick layer of mold, roots and dirt covering huge fallen trees. The logs had been in place for a considerable length of time, and were heavily overgrown by vines and roots that were in turn covered by humus, detritus, and dirt, all forming a layer about four to six inches thick. The area in which the logs were found was swampy, with the entire layer across the log very wet. The caecilians live in the detritus layer between it and the surface of the log. The technique used for collecting the animals was to chop through the layer at two points about three feet apart. Then a horizontal cut was made in the layer low on one side, and the entire layer then rolled across the log like a carpet. The caecilians were exposed on the log surface as the layer rolled away from them, and were easily picked up. On several occasions there were three or four individuals on a single log. *C. orientalis* was found more frequently than *E. p. petersi.*

This species is uniform brownish in life.

Epicrionops sp.

A larval specimen, JAP 6690, measuring 107 mm in total length, is from Morena-Santiago Province.

The tail length is 7.2 mm, the body width 7 mm, the head width 3.2 mm. A gill slit is present, relatively large, with a small diagonal flap preceding, and one following, the diagonal opening. Preceding the slit are small gill filaments not yet absorbed. There is a lateral stripe, 1.8 to 2.1 mm wide, reaching from vent to head, continued along the upper jaw to below the eye, where it widens. We do not discern a tentacular opening and presume that the tentacle has not yet perforated the surface.

This specimen was caught by Peter

Spoecker. It was found under a rock in an extremely moist area within a clearing for a "tambo" (inn) called Mirador, on the mule trail between Sevilla de Oro and Méndez. The altitude is approximately 1980 m, on the eastern slopes of the Andes. The general area is quite heavily forested, although the slopes are precipitous, and the only cleared areas are found in the immediate vicinity of tambos, so it seems likely that this is a forest species.

When first caught, the specimen was uniform dark brown. When it was killed for preservation, however, the distinct light yellow area appeared dorsolaterally.

Since we lack a number of adult characters and since we are unable to count accurately the annular folds, we hesitate to place a name on the form. The coloration and markings, however, suggest that it may be either *Epicrionops subcaudalis* or, not impossibly, *E. laticaudalis,* and would thus represent a fourth species of the genus for Ecuador.

Family **Typhlonectidae**

Of the four genera recognized in this family (*Typhlonectes, Chthonerpeton, Nectocaecilia,* and *Potamotyphlus*), only *Potamotyphlus* is certainly known from Ecuador.

Potamotyphlus kaupii (Berthold)

Caecilia kaupii Berthold, Nachr. Gesel. Göttingen, 1859, p. 181 (type-locality, Angostura [= Ciudad Bolívar], Venezuela).

Potamotyphlus kaupii Taylor, The Caecilians of the World, 1968, pp. 257-263, figs. 130, 131.

One specimen, USNM 811 from "Pucayacú entre Montalvo et Sarayacú Río Bobonaza, Pastaza Province, Ecuador," is the only record of the species in Ecuadorian waters known to us.

The following characters are evident: Length about 442 mm; body width about 10.4 mm; body (compressed) height, 17.2 mm; head width, 8.2 mm. There are 93 primaries and no secondaries. The teeth are premaxillary-maxillary, 24-1-24; prevomeropalatine, 19-1-20; dentary, 24-24; splenial, 5-4+. The terminal fin reaches a height of 3 mm. The terminal 10 mm of the animal is unsegmented. The general color of the specimen is brownish, distinctly lighter on sides and venter; the edges of the folds are bordered by black lines.

The development of the enlarged clasping organ in the tail of the male, the character of body segmentation, and the reduced head size of this species seem to warrant its recognition in the genus *Potamotyphlus* Taylor.

The black lines bordering the well-defined folds, and the diminutive head of this aquatic species will likewise identify the female, although lacking the large clasping organ.

Family **Caeciliidae**

This family is represented in Ecuador by four genera: *Siphonops, Microcaecilia, Oscaecilia,* and *Caecilia.* The last genus, the largest in numbers of species in South America, has representatives of three of the largest species of the order. There are approximately a dozen species known in Ecuador.

One of us (Taylor, 1968) has recently proposed separating the family Caeciliidae into two subfamilies, the *Caeciliinae,* composed of the large-toothed *Caecilia* and *Oscaecilia,* and the remainder of the genera in the subfamily Dermophiinae.

Siphonops annulatus (Mikan)

Caecilia annulata Mikan, Delectus florae et faunae Brasiliensis . . . Vidabonae, 1820, folio, pl. II (type-locality, Sebastianopolis, Brasil).

Siphonops annulatus Wagler, Isis von Oken, Band 21, Heft 7, 1828, p. 742, pl. 10, figs. 1-2, Taylor, The Caecilians of the World, 1968, pp. 555-560, figs. 301, 301a, 302.

This species, the most widely distributed form of the order known in South America, is confined to areas draining into

the Atlantic or Caribbean. It is not known in the Transandean regions draining into the Pacific. The ability of the species better to withstand desiccation seemingly is responsible for this distribution since it is reputedly found, at least occasionally, in relatively dry situations; also it would appear to utilize a somewhat greater variety of food which also might be a factor.

The variation in statistical data and color in the widespread populations is relatively small.

Our specimen, USNM 160367, from the mouth of the Río Copataza, Napo Province, Ecuador, shows the following characteristics: length 329 mm; body width, about 24.5 mm; width in length, approximately 13 times; primary folds, 92, complete save for the terminal folds which are incomplete above; premaxillary-maxillary teeth, 14-1-14; prevomeropalatine, 14-1-14; dentary, 12-12; no splenial teeth. No scales present.

The uniform basal coloration of gray to ultramarine with white bands bordering the folds make this one of the most conspicuous and easily identified species.

Microcaecilia albiceps (Boulenger)

Dermophis albiceps Boulenger, Catalogue of the Batrachia Gradientia *s.* Caudata and Batrachia Apoda in the collection of the British Museum, 2nd ed., 1882, p. 98, pl. 8, fig. 1, 1a (type-locality, "Ecuador").

Microcaecilia albiceps Taylor, The Caecilians of the World, 1968, pp. 533-538, figs. 290, 291.

The close similarity between the type and specimens from the eastern slope of the Ecuadorian Andes suggests that the type originated in that area also.

While this is a common species, none has been found on the western, Pacific drainage of the country.

Oscaecilia bassleri (Dunn)

Caecilia bassleri Dunn, Bull. Mus. Comp. Zool. Harvard College, vol. 91, 1942, pp. 518-519 (type-locality, Río Pastaza, Ecuador).

Oscaecilia bassleri Taylor, The Caecilians of the World, 1968, pp. 600-605, figs. 327-330.

This species, originally described in the genus *Caecilia,* has been placed in the genus *Oscaecilia* Taylor since the type-specimen differs from the other Ecuadorian species of the genus *Caecilia* in having a solid skull with the eye pushed close to the brain and covered with bone.

Three specimens of this species are present in our material from Ecuador. These are USNM 160368 from Río Conambo, Pastaza; USNM 160369, headwaters of Río Bobonaza, Pastaza; and JAP 7803, Río Arajuno, Napo.

The species is known from numerous other localities.

Oscaecilia equatorialis Taylor

Oscaecilia equatorialis Taylor, Univ. Kansas Sci. Bull., vol. 50, no. 5, 1973, pp. 221-224, figs. 34-36 (type-locality, Dyott Farm, Km 121 from Quito, 6 km east Santo Domingo de los Colorados, Pichincha Province, Ecuador).

The eye is covered with bone but is visible through the bone when the skin above it is lifted. The tentacular aperture is on the underside of the snout, almost directly below the nostril but much closer to the nostril than to the eye; secondary folds are present and scales occur in at least the last third of the body. Splenial teeth are present.

The following data were taken from the type, USNM 166421: Total length, 432 mm; width of body, 5 mm; width in length, approximately 86 times; width of head, 5.8 mm; eye to tentacle, 2.5 mm; tentacle to nostril, 1.0 mm. The first collar is relatively narrow without an obvious transverse groove; the second is wider than the first, without a transverse dorsal groove. Primaries, 180, complete on posterior part of body; secondaries, 10; two prominent narial plugs within the border of the anterior part of tongue, behind which the tongue shows rather short longitudinal striations; choanae of mod-

erate size, the diameter of one in the distance between choanae, 1.0 time. The nostril is dorsal, well visible from directly above head. The snout projects 1.5 mm. The formula for the dentition is: Premaxillary-maxillary, 9-1-10; prevomeropalatine, 8-1-9; dentary, 8-8; splenial, 3-3.

Color: Head yellowish olive above and below in distinct contrast to the grayish slate color of the body, with some brownish olive color on sides of neck and throat; vent and entire ventral face of terminus whitish.

The specimen is a female, but probably not full grown. Anal glands are not present. The head has been nearly severed.

This is the first report of a form of *Oscaecilia* to occur on the western slope of the Ecuadorian Andes.

Caecilia pachynema Günther

Caecilia pachynema Günther, Proc. Zool. Soc. London, 1859, pp. 417-418 (type-locality, "Western Ecuador," elevation 6200 ft.). Taylor, The Caecilians of the World, 1968, pp. 425,431, figs. 225-230.

This species would seem to be confined to western Andean areas (Pacific and Caribbean drainage) despite the fact that it has also been reported in the Amazonian drainage (Villavicencio, Colombia, and Normandia, Zunia, Río Upano, Ecuador). Dunn (1942) reported some specimens from "Perú" and certain ones lacking specific locality data. Parker (1934) reported specimens from Zamora, also on the eastern face of the Andes.

Taylor (1968) regarded the specimen from Normandia as representing a different species, *C. crassisquama,* and he referred the two Peruvian specimens to *C. attenuata.* Seemingly certain other specimens referred to this species by Dr. Dunn (1942) are open to question.

The type of *Caecilia pachynema* described by Günther gives the following data: folds on body, 168; ratio of body length to greatest diameter, 92:1. He states that the folds do not reach entirely around the body and that the body is covered all over with rudimentary scales which have more the appearance of minute granulations. The folds on the posterior portion of the body are not deeper than the others, nor do they contain any scales, as in *C. gracilis.* The upper and lower jaws are armed with five hooklike teeth directed backwards on each side, and the palate has three similar teeth on each side. I cannot find any prominences on the tongue or distinguish the eyes. The color is blackish-ash; there is a whitish blotch between every pair of folds.

Günther's description must be interpreted with care. The so-called rudimentary scales are in reality only the glands in the skin; some of the terminal folds of the body may have scales; and the given number of teeth does not take into account the group-loss of alternate teeth in the anterior part of the premaxillary-maxillary series and in the dentary and prevomerine series. At a certain time in the cycle the alternate teeth may be in place and functioning before the formerly functioning teeth are lost. There are two nearly terminal narial plugs present on the tongue. While the tentacular aperture is not mentioned, it is invariably present below the nostril on the underside of the snout in adults.

USNM 160363 is from Pucará, Imbabura Province, Ecuador, 5 km north of Apuel. The total length is 433 mm; body width, about 8.8 mm; width in length, about 49 times; eye to tentacle, 3.4 mm; tentacle to nostril, 1.2 mm; tongue with narial plugs; primary folds, 161, mostly incomplete; secondary folds, 0; premaxillary-maxillary teeth, 9-1-9; prevomeropalatine, 8-1-9; dentary, 9-9; splenial, 2-2; eye in a socket. This specimen differs somewhat from the type in that the median ventral dark stripe is incomplete so that the lateral cream or yellow spots may reach onto the venter in places.

We strongly suspect that the species is confined to the Pacific drainage.

Caecilia abitaguae Dunn

Caecilia abitaguae Dunn, Bull. Mus. Comp. Zool. Harvard College, vol. 91, 1942, pp. 508-509 (type-locality, Abitagua, Pastaza Province, Ecuador, 1100 m elevation).

This species for a considerable time has been known from only the type and two topotypic paratypes. It is a very large species, reaching a known length of 1200 mm and a diameter of about 22 mm. Taylor (1968) has recently reported two more specimens that differ from the type. One of these is from near the type-locality but it lacks traces of secondary folds. The second specimen was taken on the Cordillera del Condor at an elevation of 1280 m, Morena-Santiago, Ecuador. This is also a large specimen, 990 mm in length.

Caecilia bokermanni Taylor

Caecilia bokermanni Taylor, The Caecilians of the World, 1968, pp. 359-363, figs. 188-190 (type-locality, Chicherota, Río Bobonaza, Napo Pastaza Province, Ecuador).

In this type-description the type is stated to be No. 234 which presumably was a field number. When entered into the EHT-HMS Collection the number given was 4581, and figures 189 and 190 are so numbered. Both figures are of the same specimen.

A second specimen, EHT-HMS 10906, acquired from Ecuador is apparently a topotype.

The following characters obtain (the italicized data are from the type; measurements in mm): Length, 325, *527;* body width, 4.8, *10.2;* body height, 6.3, *?;* primary folds, 190, *192;* secondaries, 16, *15;* premaxillary-maxillary teeth, 6-1-7, *10-10;* prevomeropalatine teeth, 8-1-8, *8-1-8;* dentary teeth, 8-8, *10-10;* splenial teeth, 2-2, *2-2;* width in length, 67.5 times, *51.5* times.

Caecilia orientalis Taylor
(Fig. 1)

Caecilia orientalis Taylor, The Caecilians of the World, 1968, pp. 417-425, figs. 220, 224, 224a (type-locality, La Bonita, Napo Province, Ecuador, elevation 1935 m).

As stated in the type-description of this species, the material obtained by the junior author in Ecuador represents two populations that seem to differ chiefly in the presence of a few incomplete rows of scales posteriorly. In one lot, obtained for the most part near the headwater of Río Aguarico at La Bonita, Napo Province, 1935 m elevation and La Alegría, Río Chingsac, most of the specimens have a few scales in the terminal folds. No trace of scales is to be discovered in the second lot from Baeza and Borja in the upper drainage of the Río Napo in the province of Napo. The first lot, however, has certain specimens also lacking these scales. USNM 160350 varies from the norm of coloration in having light areas on the sides, almost contiguous so that there is an indefinite light stripe, vaguely broken at the folds since the grooves marking the primaries are slightly darker than the stripe that extends from the lower jaw to near the terminus of the body. USNM 159792 has the ventrolateral regions distinctly lighter than the dorsum, each fold having somewhat irregular dim spots reaching from midway on the sides to the venter and separated from each other by a darker slate-gray line.

The habitat for this species is the same as that for *Epicrionops petersi petersi* (*q.v.*). *Caecilia orientalis* is considerably more common than *E. p. petersi,* however, and was collected in several additional places. We took them under rocks in the yards of houses, and under smaller logs in very wet pasture land. In the latter case, the animals seemed to prefer the wettest logs and were often in the mud under the logs. They burrowed into a log

FIG. 1. *Caecilia orientalis* Taylor. Paratype. JAP 4553. La Alegría, Río Chingoac, "elevation 6248 ft." Dorsal, lateral and ventral views of head and neck region; dorsal and ventral views of terminal region.

only when it was very rotten, pulpy, and extremely wet.

The animal is a solid blue color in life.

The electrocardiogram of this species was described in some detail by Peters and Mullen (1966) under the name *Caecilia guentheri* (W. Peters).

Caecilia crassisquama Taylor

Caecilia crassisquama Taylor, The Caecilians of the World, 1968, pp. 369-370, fig. 193 (type-locality, Normandía, Zuñia, Río Upano, Ecuador, 1400-1800 m elevation; eastern slope of the Andes, Amazonian drainage).

This large species lacks traces of secondaries, but has bony, inflexible scales in the posterior folds. Practically all folds are incomplete above and below. A lateral yellowish stripe is present. It is known only from the type-locality.

Caecilia disossea Taylor

Caecilia bassleri Dunn (*part.*), Bull. Mus. Comp. Zool. Harvard College, vol. 91, 1942, pp. 518-519 (excluding specimens with eye sockets).

Caecilia disossea Taylor, The Caecilians of the World, 1968, pp. 374-378, figs. 196, 197 (type-locality, mouth of the Río Santiago, Perú) (a paratype of *Caecilia bassleri*).

Two specimens were collected from the eastern Ecuadorian slopes; one, USNM 160364, from Río Pucunó, Napo Province; one, USNM 160366 ♂, from Cabeceras del Río Napo, Napo Province, Ecuador.

Caecilia dunni Hershkovitz

Caecilia dunni Hershkovitz, Occ. Papers Mus. Zool. U. Michigan, No. 370, 1938, p. 2, fig. 1 (type-locality, near Tena, Napo Province, Ecuador, 1700 ft. elevation). Dunn, Bull. Mus. Comp. Zool. Harvard College, vol. 91, no. 6, 1942, p. 500. Taylor, The Caecilians of the World, 1968, pp. 378-381.

Dunn recorded a second Ecuadorian specimen, BMNH 98.3.1, Cachabe, N.W. Ecuador, that was reputed to have only 38 secondaries. Neither of us has examined this specimen.

Caecilia nigricans Boulenger

Caecilia nigricans Boulenger, Ann. Mag. Nat. Hist.,

ser. 7, vol. 9, 1902, p. 51 (type-locality, Río Lita, 3000 ft. elevation, northwest Ecuador [Pacific drainage]).

This very large species ranges along the Pacific Andean slope and coast of northern Ecuador and Colombia; in the cuenca of the Río Atrato; and extends into eastern Darień, Panamá. Presumably it is confined to these Pacific and Caribbean drainage areas.

One specimen, JAP 8257, collected about 10 km north of Mindo on the road to Puerto Quito, Ecuador, has the following characters: Length, approximately 800 mm; body width, 24 mm tapering to 19 mm near terminus; width in length, about 33 times; primary folds, 133; secondary folds, 16. Scale rows, 1 in each fold, irregular posteriorly; scales begin about 40th fold; subdermal scales present; eye in socket.

The head has been injured and the dentition of the upper jaw is not known. The dentary teeth are 11-(11) with numbers 1, 3, and 5 functioning, indicating group loss and replacement of the teeth. The splenials are 3-2.

The larger scales posteriorly are leathery and reach a diameter a little above 3 mm. Occasional scales may be folded or krinkled.

This individual was found dead on the road at about 2:30 p.m. on a dark day during a drizzling rain. The road was under construction at the time, through an area of forest at about 1500 m altitude, and there was a considerable amount of debris and trash scattered about on both sides of the road. The forest in the area was newly cleared.

The specimen was uniform dark brown when picked up.

Caecilia albiventris Daudin
(Fig. 2)

Caecilia albiventris Daudin, Histoire Naturelle Generalle et Particulere des Reptiles, vol. 7, 1802, pp. 423-426, pl. 92, fig. 1 (type-locality, "Surinam").

Until recently this form has been placed as a synonym of what is now regarded as *Caecilia tentaculata* Linnaeus. Taylor (1972), however, has recently resurrected *albiventris* and figures are given. It is a wide-spread species, occurring from Dutch Guiana to Ecuador.

We figure a specimen, USNM 111968, from Santa Cecilia, Napo Province, 340 m elevation.

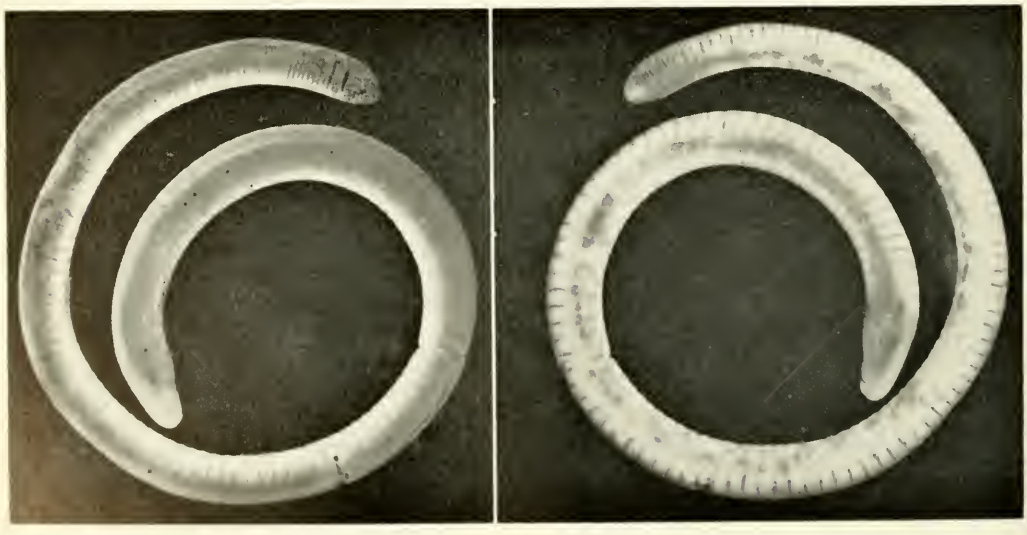

FIG. 2. *Caecilia albiventris* Daudin. USNM 111968. Santa Cecilia, Napo, Ecuador, elev. 340 m. Dorsal (left) and ventral (right) views.

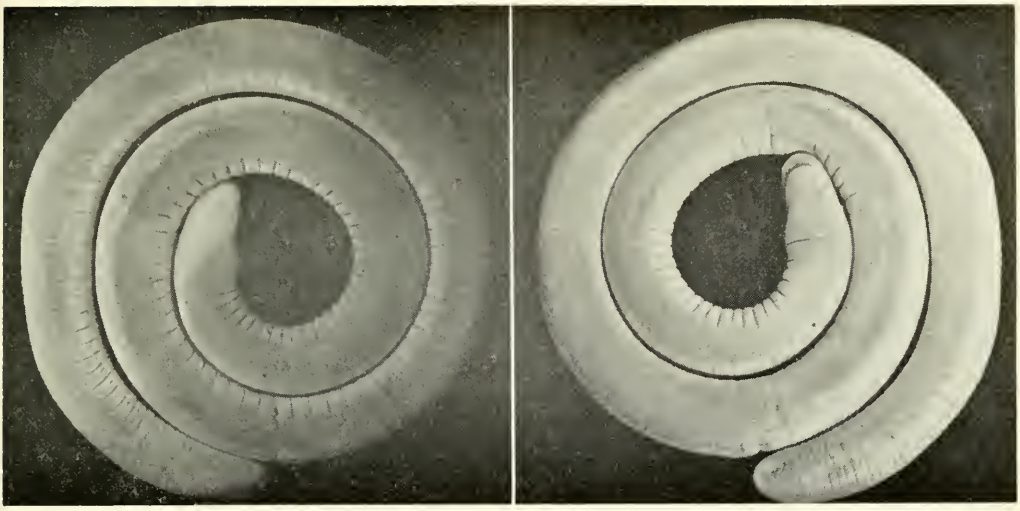

Fig. 3. *Caecilia tentaculata* Linnaeus. JAP 2066. Two km E Vera Cruz, Pastaza, Ecuador, "3300 ft. elev." Dorsal (left) and ventral (right) views. The photo at right is much lighter than the actual light slate color of the ventral surface.

Caecilia tentaculata Linnaeus
(Fig. 3)

Caecilia tentaculata Linnaeus (*part.*), Systema Naturae, ed. 10, 1758, p. 229 (type-locality, "America" [Surinam]). Taylor, The Caecilians of the World, 1968, pp. 442-448, figs. 236-238.

This species seemingly has a wide range. It has been reported throughout northern South America (Surinam, Venezuela, Colombia, Ecuador and perhaps Perú). *C. albiventris* Daudin has long been placed in the synonymy of this species. The type of Daudin's species had a length of "1 pied, 8 pouc, 5 lign" (approximately 498 mm). The type catalogue of the Paris Museum (Guibé, Catalogue des types d'amphibiens du Muséum National d'Histoire Naturelle, without date) records No. 840 as the type of *Caecilia albiventris* Daudin. This specimen measures 620 mm, a difference of approximately 120 mm. This fact throws some doubt on this specimen as the type of *albiventris* Daudin.

Our two specimens (USNM 160370, Upper Río Bobonaza, Pastaza Province, and JAP 2066, 2 km east of Vera Cruz, Pastaza Province, 1006 m) provide the following data (nos. 2066 and 160370, respectively): Length, approximately 1025, 510 mm; body width, 32, 17 mm; width in length, 32, 28 times; primary folds, 124, 123; secondary folds, 62, 57; scales begin about 30th, 34th fold; scale rows complete or partial, 1, 1; subdermal scales, none found in either; eye visible in socket in both; teeth: premaxillary-maxillary, 11-1-11, 12-1-12; prevomeropalatine, 11-1-11, 10-1-10; dentary, 10-11, 13-13; splenial, 3-3, 2-(?).

JAP 2066 was found lying beside a trail made of small logs laid crosswise, often with standing water between the logs, and had obviously just been hit with a machete a few moments before. Since the time of collection was shortly before noon, the animal had been out and crawling on the surface during the day. The area is one of heavy tropical rain forest.

The animal was fairly uniform light blue when found.

Caecilia sp.

A male specimen, JAP 1931, Pichincha Province, is left unidentified. This pre-

sents the following data: Total length, 633 mm; width of body (average), 11 mm; greatest width of head, 8 mm; eye to tentacle, 3.7 mm; tentacle to nostril, 1.2 mm; first collar with a dorsal and ventral transverse groove; second collar with a dorsal transverse groove, fused ventrally with the first primary.

Primary folds, 158, all folds seemingly complete; 5 or 6 short irregular secondary folds, none complete. Scales in posterior part; never more than one row of scales in a fold; eye in a socket, not visible externally. The tentacle below and slightly behind nostril. The palate and jaws are badly damaged; the teeth, however, can be counted as follows: premaxillary-maxillary, 10-1-11; prevomeropalatine, 10-1-11; dentary, 10-10; splenial, 3-3.

This individual was picked up in a roadside ditch in the town of Chiriboga, at 1863 meters elevation. It had been killed prior to collection, probably on the road, and had deteriorated slightly when found. The general area is one of forest and cleared forest, with parts still fairly heavily wooded. The entire area was very wet rather constantly during the rainy season.

Caecilia attenuata Taylor

Caecilia attenuata Taylor, The Caecilians of the World, 1968, pp. 358-359 (type-locality, Perú).

A recent specimen of this species is KUMNH 143556, collected by Bruce McBride 10.4 km N of Santa Rosa, Napo, Ecuador and reported by Taylor (1973).

Caecilia sp.

Two specimens from Girón, Azuay Province, at 2110 meters elevation on the Pacific slope of Ecuador offer difficulties in finding the proper species with which to associate them. They have a large number of primary folds (above 200), and lack secondaries, but have scales present in the two or three terminal centimeters of the body. There is a series of yellowish spots on the sides—a pair on each fold. The tentacle is below the nostril and the eyes are in sockets.

It is possible that they are related to *C. attenuata,* a Peruvian form from unknown specific locality (*vide supra*). They agree in having a faint line of lateral spots, the grooves between them darker. The general brownish color of the body of *attenuata* may be due to preservation; the primary folds are 186-192 (as compared to our specimens with 211-215). *C. attenuata* has no scales, while scales are present in our specimens. The width in length of *attenuata* is 62-66 times, in our specimens, 86-90 times.

Compared with *pachynema,* a species known to occur on the western slope, there is a difference of more than 50 primary folds; occasionally a few secondaries are present in *pachynema* in which case a few scales may be present also.

Data from these specimens, JAP 3531 and 3532, respectively, follow (measurements in mm): Total length, 644, 495; width of head, 7.5, 7.1; width of body, 7.5, 5.5; width in length, 86, 90 times; preanal width, 6, 4.3; eye to tentacle, 3.2, 3; tentacle to nostril, 1.2, 1; first and second collars each with a dorsal transverse groove; primary folds, 211, 215; secondaries, 0, 0.

The eyes of both are in sockets but are not visible externally, except for a slightly lighter area above them.

The dentition is premaxillary-maxillary series, 9-1-8, 9-1-8; prevomeropalatine, 10-1-10, 10-1-10; dentary, 9-1-9, 11-10; splenial, 2-2, 3-2. Scales are present in at least the last two centimeters of the body preceding the vent. The unsegmented terminal "shield" is relatively elongate.

These two specimens were found together under a single rock in soft muck, in a cleared, comparatively level area of spring seepage. The whole area was very wet and spongy, and there were several

small standing pools of water. The surrounding region was dry, with the vegetation consisting of scattered trees, low shrubs, agave fences and occasional cacti.

In life, these animals are almost totally jet black. A small region of the belly is purplish-white. In preservation they are now dark slate-gray dorsally with a lighter spot low on the sides. There is a grayish ventral stripe; laterally the folds are edged in slate-gray.

Caecilia subterminalis Taylor

Caecilia subterminalis Taylor, The Caecilians of the World, 1968, pp. 437-442, figs. 232-235 (type-locality, "Ecuador").

This specimen was obtained by exchange with Prof. Orcés of the Escuela Politechnica Nacional, Quito, Ecuador. It is clearly marked by a continuous lateral cream stripe the length of the body.

Caecilia tenuissima Taylor

(Fig. 4)

Caecilia tenuissima Taylor, Univ. Kansas Sci. Bull., vol. 50, no. 5, 1973, pp. 219-221, figs. 32, 33 (type-locality, Guayaquil, Ecuador).

Only the type, USNM 12353, is known.

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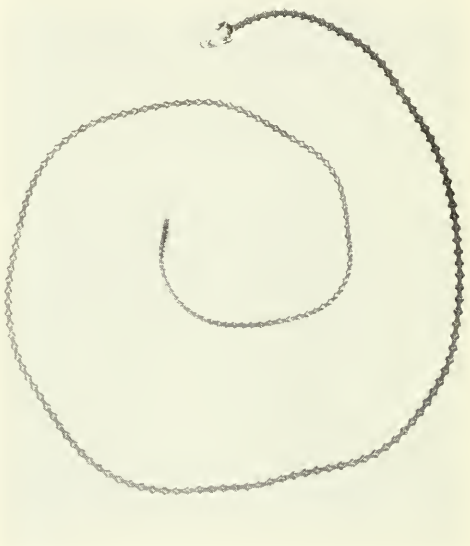

Fig. 4. *Caecilia tenuissima* Taylor. X-ray of type, USNM 12353. 186 folds; 191 vertebrae.

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THE STATUS AND FAUNAL AFFINITIES OF THE SUMMER BIRDS OF WESTERN KANSAS

By

JAMES D. RISING

Vol. 50, No. 8, pp. 347-388 June 28, 1974

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The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 50, No. 8, pp. 347-388 June 28, 1974

The Status and Faunal Affinities of the Summer Birds of Western Kansas

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ABSTRACT

Observations on the distribution and abundance of the summer birds in the western one-third of the state of Kansas are presented. Aspects of the breeding biology, especially of the commoner species, are discussed and whenever possible the current status of a species is contrasted with that of historical times in order to shed light upon the effects that modern agriculture and other environmental modification have had upon the biota.

The faunal affinities of the bird species are examined. Most of the populations of birds living in woodlands in that region are derived from species whose primary center of distribution is in eastern North America, whereas the species of birds found in grasslands or in xeric shrub are more predominantly western. Western species especially are found at the most arid sites which are commonest in the southwestern corner of the state.

There does not appear to have been any great change in the distribution and abundance of the birds inhabiting woodlands in recent times, although several southeastern species are extending their ranges westward along the Cimarron drainage. On the other hand, a large percentage of the grassland-inhabiting species that formerly occurred appear to have been extirpated. This would seem to be related to modern changes in land use rather than changes in climate.

INTRODUCTION

As European men progressively settled North America they avoided, initially at least, the "treeless" Great Plains. To the early pioneers from the forested east, ". . . all the land west of the Missouri River was barren and worthless, and . . . would forever remain so. It was . . . the abode of Indians and of wild beasts; . . . the buffalo roamed over its vast plains; and it commonly bore the name of 'The Great American Desert'" (von Richthofen, 1964: 3). The early trappers crossed the Plains to reach the mountains; the early farmers crossed the Plains to reach the west coast.

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Soon after the American Civil War the U.S. Army expelled the nomadic Indians from the Plains; they were aided in this by early cattlemen, and by hunters who decimated the bison upon which the Plains tribes depended for food. These events opened the region to a succession of agrarian settlers. First to arrive were the cattlemen who took advantage of the open range to raise herds of cattle that were ultimately driven across the prairies to railheads at Kansas City, Abilene, or Ellsworth. The windmill and barbed wire, however, made possible the smaller ranches and farms that soon preempted much of the open range. Planted "shelter belts" reduced the ferocity of the persistent winds. The transition in agricultural practice took place in a remarkably short period of time: barbed wire was available by 1874, and fenced, homesteaded ranches and farms replaced open range a few years thereafter; by the turn of the century the region was probably more densely populated in rural areas than it is today, as smaller units of land (160 or 320 acres) were homesteaded than could support families dependent on agriculture in that region. The open range was divided, fenced, and in many places farmed by settlers who appreciated the relative ease with which the "treeless" and "rockless" Plains could be farmed (Webb, 1931).

The western portion of the Great Plains, the High Plains, including western Kansas (Fig. 1), however, was too arid to permit much land use other than ranching and dry farming. At least early in the twentieth century, and to some extent today, this region was seriously overgrazed and overfarmed, sometimes resulting in severe erosion and major changes in the biota.

The present work is, in part, an attempt to describe some of these biotic

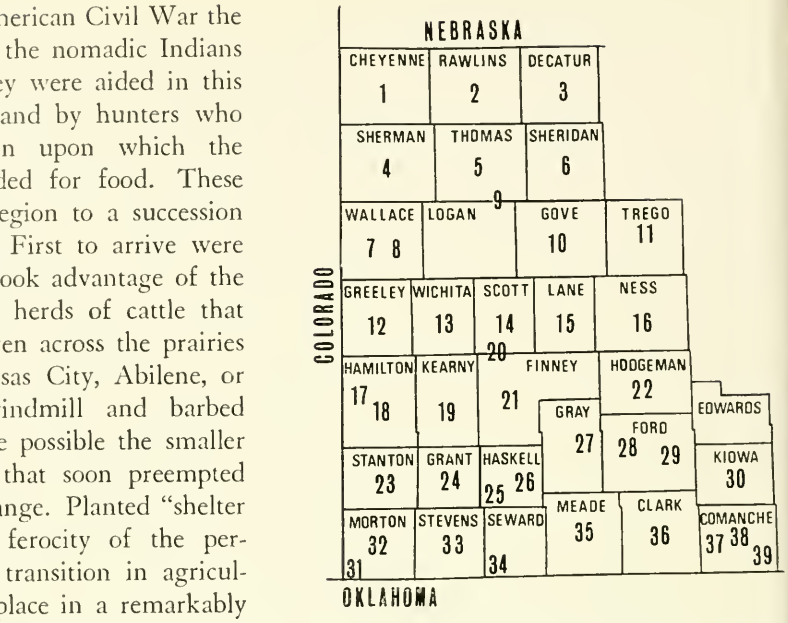

FIG. 1. Western Kansas, showing the approximate locations of larger cities and some other sites mentioned in the text. 1, St. Francis; 2, Atwood; 3, Oberlin; 4, Goodland; 5, Colby; 6, Hoxie; 7, Sharon Springs; 8, Wallace; 9, Oakley; 10, Gove; 11, WaKeeney; 12, Tribune; 13, Leoti; 14, Scott City; 15, Dighton; 16, Ness City; 17, Coolidge; 18, Syracuse; 19, Lakin; 20, Friend; 21, Garden City; 22, Jetmore; 23, Johnson; 24, Ulysses; 25, Satanta; 26, Sublette; 27, Cimarron; 28, Dodge City; 29, Ford; 30, Greensburg; 31, Elkhart; 32, Richfield; 33, Hugoton; 34, Liberal; 35, Meade; 36, Ashland; 37, Protection; 38, Coldwater; 39, Schwartz Canyon.

changes—specifically those of the avifauna—and to document the current status of birds in the western Kansas area so that future assessments of such changes will be possible. My field work in the High Plains, mostly in western Kansas (conducted from 1963 through 1968), forms the basis of this report. I have not, however, hesitated to use the literature (especially for historical perspectives) and other relevant information. This is not offered as a complete or definitive list, but rather as an account of the biology of the common birds of a portion of the Plains, an area transitional between the west and east, one recently modified by

man, and sensitive to ecological disruption.

ACKNOWLEDGMENTS

I am indebted to many people whose help and cooperation made this paper possible. Among these are many land owners who allowed me to collect and study birds on their lands; among many are Tom Finney (Meade), Maurice Barr (Liberal), Clifford Low (Coolidge), Jim Cowgill (Garden City), Clarence Hardin (Oakley), and Ernst Holste (Ludell). Further, many people accompanied me in the field at various times, and some of their observations are reported herein. Among these are: Ted Anderson, Jim Dick, Jim Hale, Jerry Jackson, Delbert Kilgore, Bill Klitz, Dave Niles, John and Trudy Rising, and Sievert Rohwer. Leila Gad kindly helped me with plant nomenclature. Jon Barlow, Roger Hansell, Dave Niles, Trudy Rising, and Fred Schueler have read all or parts of various manuscript copies, and have offered many useful suggestions. Funds have been received from the Frank M. Chapman Memorial Fund, the Kansas Academy of Sciences, The University of Kansas Department of Zoology and Museum of Natural History, and from National Science Foundation grant GB-4446X (W. A. Clemens, principal investigator) for support of studies in Systematic and Evolutionary Biology.

COMMENT ON NOMENCLATURE USED

Two desirable features of zoological nomenclature, as stated in the "Preamble" to the (1961) *International Code of Zoological Nomenclature* (Mayr, 1969: 30), are (1) to achieve ". . . stability and universality in the scientific names of animals . . . ," without (2) restricting ". . . freedom of taxonomic thought or action." It is obvious to most biologists that the system of nomenclature most widely used today for species taxa cannot, by virtue of attempting to indicate relationships "at the generic level," be stable. To believe otherwise is to assume as Linnaeus did that objective genera exist in nature and need only be discovered by biologists. Genera, of course, are artificially delimited groups of species, and the delimitation of these groups should and *will* continue to change as new data (and indeed philosophies!) emerge and the old are reassessed. This is, in my mind, the positive part of taxonomic science. We should not wish it an early end. Many biologists, however, understandably become fatigued with the *nomenclatural* chaos associated with generic restructuring and are reluctant to act as their data would suggest. For example, apparently the major objection to "lumping" many genera of "sparrows" is the attendant loss of many well-known names. People tend to be conservative about changing their language; they should not let this conservatism (by definition, at least) guide their scientific thinking. This is *one* way that binominal nomenclature restricts the freedom of both taxonomic thought and action. Another is that it does not permit the use of overlapping genera, as many systematists would like. Michener (1964) discussed these same matters in detail, and proposed that people consider a uninominal nomenclature that would reduce the apparent information content of the binominal by removing the implication of generic allocation. Such a uninominal name could be formed by hyphenating the current binominals, thus: *Icterus galbula* (Genus *Icterus*) becomes *Icterus-galbula* (genus, as with other higher categorical placement, not indicated). Such a simple modification would do much to stabilize nomenclature, and would reduce the interference of nomenclature with more important matters. In this paper I have used uninominal names so that people can assess their desirability. I have formed

these by hyphenating binominal combinations in the A.O.U. Check-list of North American Birds (1957 edition).

PHYSICAL ENVIRONMENT

The Plains are inclined, tipping from the Rocky Mountains to the Mississippi River. The upper soil strata are primarily layers, of varying thickness, of sediments washed out of the mountains and deposited on a mantle of marine rock (Webb, 1931). These sediments are relatively undissected in the arid western portion of the Great Plains (the High Plains) except in a few regions, especially along the Smoky Hill River where the marine sedimentary deposits have been secondarily exposed by erosion. Western Kansas is in these High Plains. Elevations in the Great Plains range from about 1,000 ft. (ca. 305 m) in some eastern areas gradually increasing to over a mile high at the base of the mountains in Colorado. Western Kansas ranges in elevation from just under 2,000 ft. (ca. 610 m) to 4,026 ft. (ca. 1,227 m) (Mt. Sunflower in Wallace County). Topographically the country is flat or of small rolling hills, with small canyons or valleys carved out of the soft sedimentary substratum along many of the watercourses.

There is little precipitation in the region, most occurring in the summer months (Fig. 2); thundershowers are common and account for much of the total precipitation, and much of the water that falls during storms quickly runs off. In general the average precipitation decreases from east to west (Fig. 3). High winds are characteristic; those in the Texas and Oklahoma panhandles and in southeastern Colorado and southwestern Kansas are as high as in any inland region in the United States (Webb, 1931). The

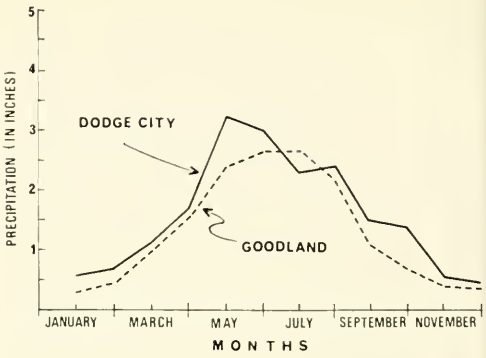

FIG. 2. Average monthly rainfall at two stations in western Kansas, 1951-1960 (from U.S. Weather Bureau data).

wind, coupled with the general aridity and high summer diurnal temperature (frequently over 100°F in southwestern Kansas), makes the potential evaporation, especially in the southern Plains, far exceed the rainfall (Fig. 4). Nonetheless, unless overgrazed, the prairie grasses trap moisture and their root systems hold soil and retard wind erosion.

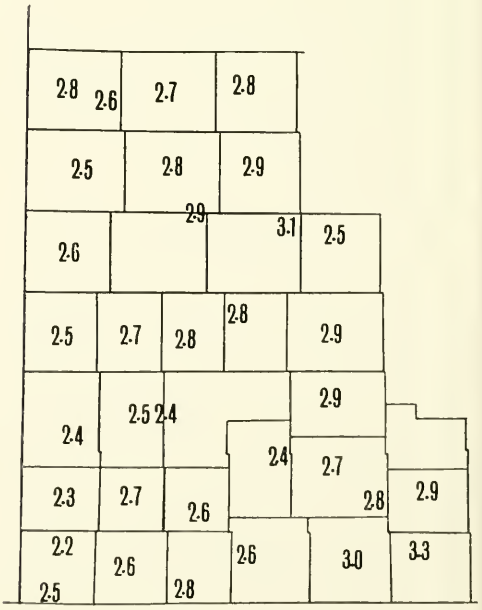

FIG. 3. Average June and July monthly rainfall (in inches) at 34 stations in western Kansas, 1951-1960 (U.S. Weather Bureau data).

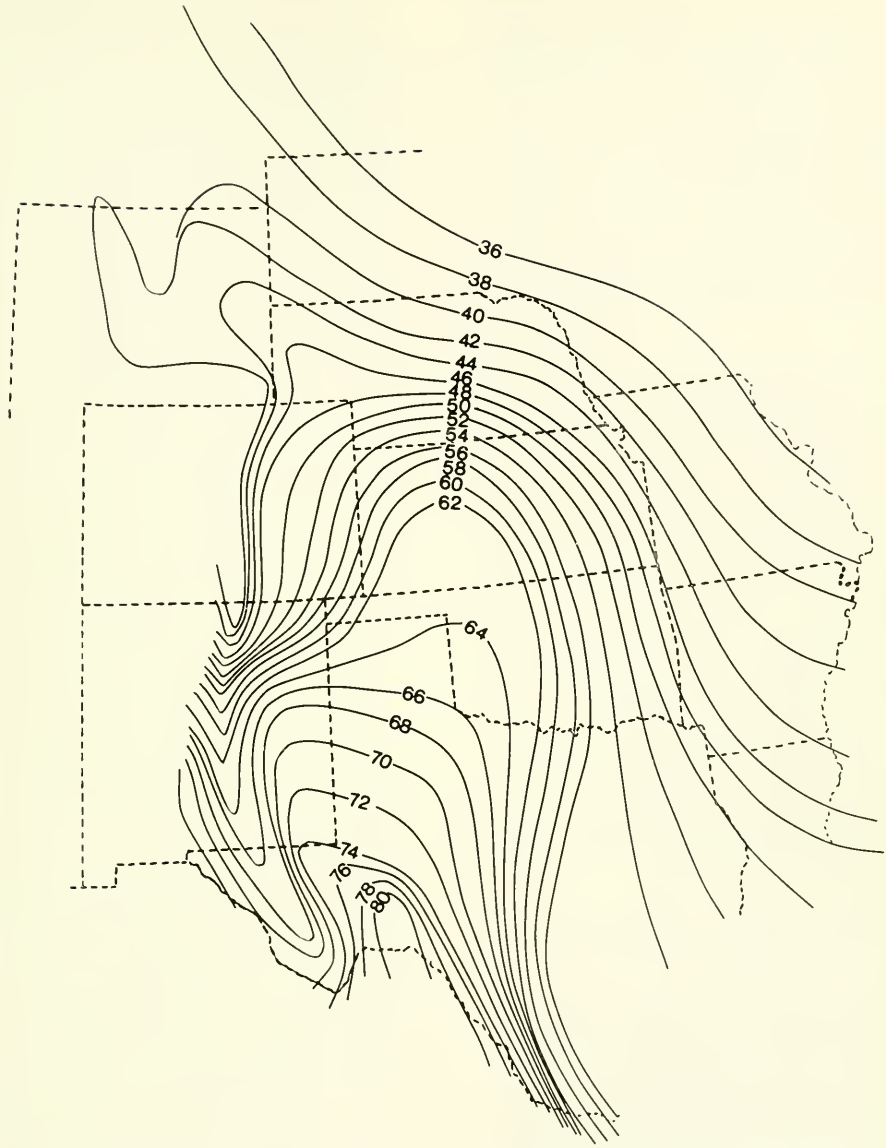

FIG. 4. Average annual lake evaporation isopleths (in inches), 1946-1955 (U.S. Weather Bureau data).

VEGETATION

Much of western Kansas is, or was in pre-agricultural times, grassland. In most places the native grasslands were of short-grass configuration with *Bouteloua-Buchloe* or *Bouteloua-Buchloe-Aristida* being dominant assemblages. Some regions, especially in the sandy soils south of the Cimarron and Arkansas rivers, originally supported *Aristida-Andropogon-Munroa* tallgrass prairie (Gates, 1937). Today grain crops (especially wheat) are widely grown in the Plains, but much grassland persists as pasture. These grasslands, however, are (or have been) frequently overgrazed, and there is considerable intrusion of "weed" species in most regions, especially Russian thistle (*Salsola-kali*), milk-

weed (*Ascelepias* sp.), mustards, and mallows. Additionally, sage (*Artemisia-filifolia*) grows in conjunction with *Bouteloua* and other grasses in many regions, especially south of the Arkansas and Cimarron rivers, and seems to be especially prevalent in overgrazed and otherwise disturbed areas. In especially arid years, chollas (probably *Cylindropuntia-imbricata*) grow in the extreme southwest.

The hyperbole of the Plains being "treeless" has frequently been taken literally. Indeed few if any trees grew between the river valleys in pre-agricultural days, but apparently some species (at least cottonwoods and willows) have always grown in places along many of the major watercourses.

Allen (1872a: 131-133) provides what is perhaps the best description of the flora of western Kansas before it was greatly altered by European man. Even though he writes of an area just east of that covered in this paper (Ellis County, Kansas), some of his observations are germane here:

> . . . The timber here is not only confined to the immediate vicinity of the streams, often to their beds, but generally occurs in thin, irregular belts or scattered clumps, and ceases entirely a few miles to the westward. The Smoky [Hill River] is already quite destitute of trees as far west as Fort Hays, and they soon disappear from the Saline. The belt of timber along Big Creek . . . afforded by far the richest field [for woodland birds]. . . . The trees [there] consist mainly of the white and red elms, and the ash-leaved maple, cottonwoods, black-walnut, and ash. Most of these trees assume a spreading form, and grow to a large size. There is little undergrowth, except where the first growth has been removed. . . .
>
> The "Plains" are here, as usual, somewhat rolling broad level plateaus, being separated by low ridges, or broken by sharp ravines and moist hollows. They are covered with short grass, usually but two or three inches high, except in the hollows and near the streams, where it often grows to the height of one or two feet. . . . During May and much of June . . . the fresh young grass is thickly dotted with a variety of showy flowers. . . . Most characteristic among them are *Malvastrum coccineum* [=*Sphaeralceacoccinea*] and one or two other malvaceous species, *Verbena aubletia* [=*V.-canadensis*], *Lippia,* a *Scutellaria* and an aster-like composite plant. . . . The sensitive brier (*Schrankia uncinata*) was also abundant, and *Rosa lucida* [=*R.-carolina*] was agreeably frequent along the streams.

In 1883 at least, Goss (1884) did find ". . . willows and cottonwoods thinly skirting the south fork of the Smoky Hill River . . ." as far west as Wallace, Wallace County.

Big Creek in Ellis County (described above by Allen) as well as Sappa and Beaver creeks in Decatur and Rawlins counties are sluggish watercourses with short drainages. These have rather abrupt banks cut into mud-clay soils, and are today, as apparently in Allen's time, bordered by mixed strands of deciduous trees. Along Sappa and Beaver creeks today the most conspicuous tree species are the cottonwood (*Populus-deltoides*) and an ash (*Fraxinus* sp.), but the other species mentioned by Allen are still present. Writing of his childhood (at the turn of the century) in Decatur County, Wolfe (1961) says:

> Fifty years ago both Sappa and Prairie Dog creeks were clearwater streams with many deep ponds. . . . The open range had been partly con-

> verted into farms, but much of the original prairie remained, with tall bluestem in the bottomlands and "bunch grass" (probably a species of bluestem) and buffalo grass covering the uplands. . . . [There was a] fringe of trees growing along Sappa and Prairie Dog creeks.

The mixed deciduous woodlands that grew and grow along these creeks in northwestern Kansas are unusual if not unique to western Kansas. Most other watercourses run over sandy soils, and cottonwoods, willows (*Salix* sp.), and tamarisk (*Tamarix-gallica*) are the only *common* trees along them. The larger "rivers" that cross western Kansas (Cimarron, Arkansas, Smoky Hill, Republican) are exemplary. These drain the Rockies or the Colorado High Plains (Smoky Hill, Republican) and all have rapid flow and are shallow (the Cimarron in many places is completely subterranean during much of the year west of Clark County and intermittently subterranean east of there). Several early explorers and adventurers mention these rivers and the bordering vegetation in their journals. For example G. C. Sibley, who surveyed the Arkansas and Cimarron rivers in 1825, makes frequent reference in his journal to the arboreal vegetation at many localities. While traveling along Walnut Creek, parallel to the Arkansas River, in what is now southern Barton County, Sibley wrote (Gregg, 1952: 70):

> As far as I have been able to examine this [Walnut] Creek today, it has a thin growth of Ash, Walnut, & Box Elder & Cotton Wood Timber all along its banks.

Near the present site of Dodge City, Ford County, he noted (Gregg, 1952: 77) that

> . . . the [Arkansas] River [is] full of small islands on some of the largest of which are a few Cotton Trees.

Near the present site of Hartland, a few miles southwest of Lakin, Kearny County, Sibley wrote (Gregg, 1952: 86):

> . . . all along the [Arkansas] river is blocked up with small Islands, having on them some Cotton Trees of pretty good growth. . . . Our camp is under some large Cotton Trees . . . and at the upper end of a small grove of Timber (among which are some large Willows). . . .

At that juncture Sibley's party left the Arkansas River and continued westward along the Cimarron River to the south. Arboreal vegetation must have been scarce along the Cimarron at that time (as it is in places today) as Sibley fails to mention it in most of his locality descriptions. At one place, however, probably near the present Morton-Stevens county line, he mentions ". . . old dead fallen trees . . ." (Gregg, 1952: 89). In his description of the Cimarron Valley north of the present city of Elkhart, he mentions the presence of tall grasses and "weeds" but no trees, although he did locate a ". . . small Grove of Green Cotton Trees, near some high Rocky Bluffs . . ." (Gregg, 1952: 93) farther to the west, in what must be Cimarron County, Oklahoma.

Another early prairie traveler, Jacob Fowler, traveled up the Arkansas River to the present site of Pueblo, Colorado, in the fall of 1821. His comments (Coues, 1898) are somewhat less lucid than Sibley's, but he explicitly describes cottonwoods and willows in riparian areas.

Menke (1894), writing of the Arkansas River Valley in Finney County as it appeared about 60 years later, said:

> The Arkansas river flows through the county from the west, dividing it into two divisions. The portion lying north of the river is . . . chiefly of prairies, the exception being a series

> of sand-stone bluffs in the southeast corner and a group of sand-hills near the center. The southern division is nearly all sand-hills with little variation. The western half of the river valley is partially wooded with medium-sized cottonwoods; . . . where water is obtainable, the majority of the land-owners have planted groves of fruit and other trees. . . .
>
> Heavy rains early in the spring fill the prairie lakes and convert more or less of the river bottom into swamps. . . .
>
> On the other hand a lack of rain reverses these conditions. . . .

In pre-agricultural times, several factors may have operated to exclude trees from much of the High Plains. Certainly prairie fires of natural origin or those started by Indians were a factor that must have kept trees from areas that otherwise would have supported them. Also the large herds of bison doubtless trampled down saplings, people felled trees for fuel, and perhaps floods periodically inundated them. Several of the journal entries cited above imply that it was on the islands in the rivers that the largest stands of trees grew (especially in the High Plains), and perhaps these served as refuges from which other areas could periodically be seeded. These islands would be secure from fire and doubtless were relatively out of the way for bison, but would have been exposed to flooding.

European settlers planted a variety of trees on the Plains. Around towns native cottonwoods and Siberian ("Chinese") elms (*Ulmus-pumila*) were most commonly planted, and elms, cedars (*Juniperus-virginiana*), osage-orange (*Maclura-pomifera*), white mulberry (*Morus-alba*), and Russian olive (*Elaeagnus-angustifolia*) were commonly used in hedges and shelter-belts. Individuals of these species, especially mulberry and osage-orange, have become established in places in the river valleys and, along with the introduced tamarisk, in some places form an important component of the flora. The tamarisk, especially, often grows in pure thickets, perhaps in sites where no native tree could persist.

It seems, in summary, that limited numbers of trees were characteristically associated with riparian situations even before European man controlled the prairie fires and bison which served as natural checks to trees in many sites. Along the sluggish creeks of northwestern Kansas mixed deciduous woodlands existed, whereas along the swift-flowing, shallow streams and rivers characteristic of most of western Kansas only cottonwoods and willows grew. Recent introductions have probably had little qualitative effect on these woodlands. However, planted woodlots, shelter-belts, and trees maintained in urban areas have greatly increased the total timber acreage in western Kansas. The grassland areas have been greatly modified by cultivation and overgrazing (although the bison and prairie dogs doubtless "overgrazed" in a manner comparable to that of domesticated herds), and poor land management (especially in the 1920s and 1930s) has resulted in considerable erosional loss of topsoil. Control of fires and floods has probably encouraged the growth of shrubs (as well as trees) in many areas.

FAUNAL ANALYSIS

Composition of the avifauna of western Kansas

Kansas is centrally located in North America, and not surprisingly the fauna contains an admixture of forms: many species primarily found in the east (designated here as "eastern") reach a limit to their distribution in western Kansas, as

do many "western" and "southern" species; the ranges of several primarily allopatric but ecologically comparable species (semispecies) abut in the region. Examination of the species composition at different sites, as well as the relative abundance of different species, reveals the extent to which each of these faunal elements (i.e., "eastern," "western") is represented, and this seems to be a reflection of the ecology and history of the region.

Woodland birds (that is, species that most commonly forage and nest in association with trees; Table 1) are the largest single component of the avifauna, comprising about 46% (Table 2) of the total. Johnston (1964) calculated that about 58% of the breeding birds of the entire state of Kansas are woodland species, and the apparent difference between these two approximate figures may well reflect the poorly developed and virtually unstratified woodland habitat in the western portion of the state. Most species of woodland birds are similar to species characteristic of the eastern broadleafed woodlands. Of those species that appear to be derived from western or southwestern woodlands ("red-shafted" flicker, Ladder-backed Woodpecker, Western Kingbird, Ash-throated Flycatcher, Western Wood Pewee, Black-billed Magpie, Bullock Oriole, Black-headed Grosbeak, Lazuli Bunting, Rufous-crowned Sparrow), only the kingbird, magpie and oriole are common, the others being of local or sporadic occurrence. These "western" species comprise only about 18% of the woodland avifauna (cf. about 58% eastern and southeastern, 11% southern, and 13% "unanalyzed").

Grassland and xeric scrub species are relatively well represented in the region and comprise about 23% of the total (Tables 1 and 2). Many of these species are common in favorable habitat. Statewide, these grassland and xeric scrub species comprise only about 15% of the total (Johnston, 1964), and in North America, only 10.1% (Udvardy, 1959). Species of apparent western or southwestern origin dominate the grassland-scrub assemblage and comprise about 47% of the total (cf. about 31% unanalyzed, 12% eastern, 9% northern). Of the four eastern species (Table 1) the Greater Prairie Chicken no longer occurs in the region, and the Eastern Meadowlark is of restricted occurrence; of the three northern species, the Sharp-tailed Grouse and Chestnut-collared Longspur no longer breed in western Kansas, and there is but one record of the Clay-colored Sparrow from there.

Of the limnic species (Table 1), which comprise an additional 22% of the avifauna, only the Killdeer, Belted Kingfisher, Yellowthroat, and Red-winged Blackbird are common, and thus the percentage gives a somewhat distorted impression of the significance of these forms to the ecology of the region. In fact, of the "common" breeding species of western Kansas, only 6% are limnic—a reasonable reflection of the extent to which this habitat is available to birds in the High Plains.

Because of the variation in abundance among species, it is not wholly satisfactory to analyze the avifauna in terms of species composition. Therefore, I have used census data (Table 3) on the numbers of individuals at 18 stations along western Kansas watercourses to correct for variation in density among the species. Figures 5-7 show the percentages of the numbers of *individuals* of eastern, western, and southern species. Data on the Bobwhite, Starling, and American Goldfinch are not included as they are incomplete; data on the "flickers," and Baltimore and Bullock orioles are omitted because the high frequency of phenetically intermediate in-

TABLE 1. Ecological analysis of breeding birds[1] of western Kansas.

WOODLAND		
Mississippi Kite SE[2]	Scissor-tailed Flycatcher S	Bell Vireo E
Cooper Hawk U	Ash-throated Flycatcher SW	Red-eyed Vireo E
Red-tailed Hawk E	Great Crested Flycatcher E	Warbling Vireo E
Sparrow Hawk U	Eastern Phoebe E	Yellow Warbler W
Turkey S	Eastern Wood Pewee E	Yellow-breasted Chat U
Mourning Dove U	Western Wood Pewee W	Orchard Oriole E
Yellow-billed Cuckoo E	Blue Jay E	Baltimore Oriole E
Black-billed Cuckoo E	Black-billed Magpie W	Bullock Oriole W
Screech Owl E	Common Crow U	Common Grackle E
Barred Owl E	Black-capped Chickadee E	Brown-headed Cowbird U
Long-eared Owl E	Carolina Chickadee SE	Cardinal E
Chuck-will's-widow SE	House Wren E	Rose-breasted Grosbeak E
"yellow-shafted flicker" E	Bewick Wren S	Black-headed Grosbeak W
"red-shafted flicker" W	Mockingbird S	Blue Grosbeak S
Red-bellied Woodpecker E	Catbird E	Indigo Bunting E
Red-headed Woodpecker E	Brown Thrasher E	Lazuli Bunting W
Hairy Woodpecker U	Robin E	Painted Bunting S
Downy Woodpecker U	Wood Thrush E	American Goldfinch E
Ladder-backed Woodpecker SW	Eastern Bluebird E	Rufous-sided Towhee U
Eastern Kingbird E	Blue-gray Gnatcatcher E	Rufous-crowned Sparrow SW
Western Kingbird W	Black-capped Vireo S	Field Sparrow E
GRASSLAND AND XERIC SCRUB		
Swainson Hawk W	Long-billed Curlew W	Eastern Meadowlark E
Ferruginous Hawk W	Upland Plover U	Western Meadowlark W
Prairie Falcon W	Burrowing Owl W	Dickcissel E
Marsh Hawk U	Short-eared Owl U	Lark Bunting W
Greater Prairie Chicken E	Common Nighthawk U	Grasshopper Sparrow U
Lesser Prairie Chicken SW	Poor-will W	Vesper Sparrow U
Sharp-tailed Grouse N	Say Phoebe W	Lark Sparrow E
Bobwhite E,W	Horned Lark U	Cassin Sparrow W
Scaled Quail SW	White-necked Raven SW	Clay-colored Sparrow N
Ring-necked Pheasant U	Rock Wren W	Chestnut-collared Longspur N
Mountain Plover W	Loggerhead Shrike U	
LIMNIC		
Pied-billed Grebe U	Pintail U	Killdeer U
Great Blue Heron U	Gadwall U	Spotted Sandpiper U
Green Heron U	Blue-winged Teal U	Avocet W
Little Blue Heron U	Cinnamon Teal W	Wilson Phalarope U
Snowy Egret U	Shoveller U	Least Tern U
Black-crowned Night Heron U	Ruddy Duck U	Black Tern U
Yellow-crowned Night Heron U	Virginia Rail U	Belted Kingfisher U
Least Bittern U	Black Rail U	Yellowthroat U
American Bittern U	American Coot U	Yellow-headed Blackbird W
Canada Goose U	Snowy Plover U	Red-winged Blackbird U
Mallard U		
MISCELLANEOUS		
Turkey Vulture U	Great Horned Owl U	Barn Swallow U
Golden Eagle U	Chimney Swift E	Cliff Swallow U
Rock Dove U	Bank Swallow U	Purple Martin E
Barn Owl U	Rough-winged Swallow U	House Sparrow U

[1] Summer residents or probable summer residents.

[2] Letters refer to the regions to which the western Kansas populations seem to show greatest affinities, and are abbreviations of compass directions; U = unanalyzed.

TABLE 2. Ecological composition of the breeding avifauna of western Kansas.[1]

Habitat Type	No. Species	Percentage
Woodland	63	46
Grassland and Xeric Scrub	32	23
Limnic	31	22
Miscellaneous	12	9

[1] Based on Table 1.

dividuals—reflecting some sort of intermediacy between eastern and western morphs—in this region obscures faunal relationships; and data on the shrike are omitted because the species is not strictly a species characteristic of riparian woodlands. The unanalyzed element was included when calculating percentages, but those data are not figured. The Figures show the trends elucidated by these percentages; the percentages of individuals belonging to eastern species decrease in riparian woodlands to the westward, but never fewer than nearly one-third of the

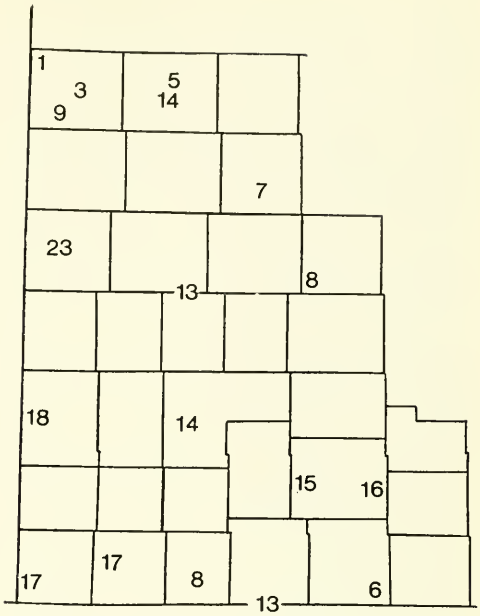

FIG. 6. The percentages of individuals belonging to western species (based on Table 3) at 18 stations in western Kansas.

individuals present in these habitats are eastern (cf. about 20% western at maxi-

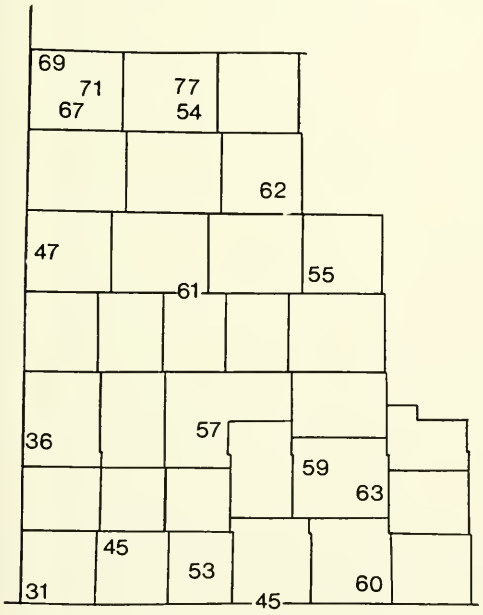

FIG. 5. The percentages of individuals belonging to eastern species (based on Table 3) at 18 stations in western Kansas.

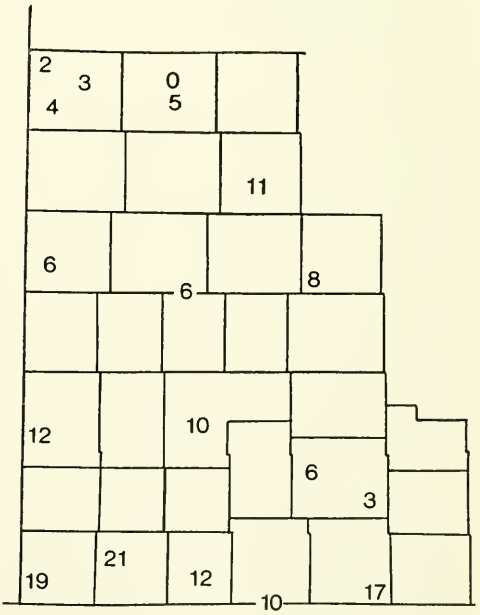

FIG. 7. The percentages of individuals belonging to southern species (based on Table 3) at 18 stations in western Kansas.

TABLE 3. Numbers of birds counted at 18 stations in western Kansas.

Species	Locality																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Mississippi Kite	10[1]	2	5	5	4	0	5	8	0	0	0	0	0	0	0	0	0	0
Cooper Hawk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Red-tailed Hawk	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0
Sparrow Hawk	2	1	1	2	2	2	3	2	2	2	2	1	1	3	2	2	2	0
Bobwhite	?	?	6	2	10	2	?	?	?	?	4	5	6	6	?	2	0	4
Mourning Dove	35	40	41	35	35	24	24	30	20	30	30	40	20	36	30	22	15	20
Yellow-billed Cuckoo	16	2	8	4	4	0	8	6	1	4	12	4	2	12	6	2	0	4
Black-billed Cuckoo	3	0	2	0	0	0	0	0	0	0	3	2	0	4	0	0	0	0
Screech Owl	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Great Horned Owl	1	2	2	2	2	0	2	1	2	2	2	1	2	0	2	0	1	3
Barred Owl	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Chuck-will's-widow	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
flicker	8	4	2	2	1	12	20	2	2	6	2	4	16	25	10	6	8	28
Red-bellied Woodpecker	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Red-headed Woodpecker	12	12	4	6	2	6	4	12	4	6	6	3	5	20	12	6	3	16
Hairy Woodpecker	4	0	1	2	1	1	2	0	4	0	0	4	1	0	2	0	2	3
Downy Woodpecker	4	6	3	0	1	1	8	0	2	2	4	4	3	3	5	4	3	3
Eastern Kingbird	12	20	20	10	6	10	10	10	10	10	20	15	20	8	20	6	8	12
Western Kingbird	16	20	15	40	12	30	24	10	10	10	25	45	6	4	6	0	12	0
Scissor-tailed Flycatcher	8	8	2	6	2	0	3	3	0	2	0	0	6	0	0	0	0	0
Great Crested Flycatcher	14	4	5	1	0	4	7	5	4	2	7	2	3	4	5	4	1	4
Ash-throated Flycatcher	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Eastern Phoebe	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1
Blue Jay	20	2	7	2	3	4	12	4	2	10	10	7	12	16	15	4	2	22
Black-billed Magpie	1	1	2	6	2	1	8	8	8	0	1	4	4	2	10	1	0	3
Common Crow	?	1	2	1	1	1	1	0	2	2	2	0	?	0	1	0	0	2
Black-capped Chickadee	0	0	1	0	0	4	6	0	2	2	5	3	4	4	5	2	1	12
Carolina Chickadee	12	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
House Wren	10	2	6	4	3	18	24	12	4	12	10	14	12	40	20	18	12	35
Bewick Wren	15	4	4	10	0	2	4	0	0	6	0	0	0	0	0	0	0	0
Mockingbird	10	4	15	24	15	2	2	10	10	4	7	13	3	0	12	0	2	0
Catbird	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2
Brown Thrasher	16	1	6	4	1	12	12	0	2	2	6	8	8	10	12	8	4	16
American Robin	0	0	0	0	0	0	1	0	0	0	0	0	2	0	4	0	0	3
Wood Thrush	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Eastern Bluebird	0	2	2	0	2	0	2	2	0	?	4	2	3	0	10	2	3	0
Blue-gray Gnatcatcher	0	0	0	1	2	0	1	1	0	0	2	1	0	0	0	0	0	0
Loggerhead Shrike	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0
Starling	?	4	4	2	1	2	?	?	?	?	6	6	4	12	?	4	?	?
Bell Vireo	1	0	3	3	0	4	0	0	0	0	0	0	1	0	0	0	0	0
Red-eyed Vireo	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Warbling Vireo	8	10	6	12	2	16	9	6	0	0	2	4	0	0	5	0	1	0
Yellow Warbler	0	0	0	8	6	0	1	6	0	1	0	0	0	0	0	0	0	0
Yellowthroat	2	4	3	1	0	4	3	0	1	1	0	2	0	8	5	0	0	6
Yellow-breasted Chat	0	1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	2
Orchard Oriole	14	20	20	50	6	36	15	30	6	25	30	30	3	32	20	12	10	24
Baltimore/Bullock orioles	40	50	50	45	40	24	30	50	30	50	35	35	8	16	20	10	10	15
Common Grackle	1	0	6	0	1	3	3	?	?	?	?	4	2	4	10	4	?	?
Cardinal	8	0	3	0	0	6	5	1	0	0	0	0	4	0	0	0	0	10
Black-headed Grosbeak	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	7
Blue Grosbeak	8	2	4	8	6	2	4	4	2	5	4	0	6	8	2	2	2	0
Indigo Bunting	8	0	1	3	2	0	3	0	1	0	0	1	2	4	0	0	0	0
Painted Bunting	8	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Goldfinch	x	x	x	x	?	x	x	x	x	x	x	x	x	x	x	x	0	x
Rufous-sided Towhee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Total No. Pairs/ca. 10 Hectares	332	232	265	304	177	239	268	223	131	192	244	264	171	282	252	121	104	262

mum). Comparable statements could summarize geographic trends in southern and western species too.

Two separate censuses were conducted in Rawlins County. On one, taken in rank mixed deciduous woodlands along Beaver Creek, 77% of the individuals were representatives of eastern species (cf. 5% western; see Figs. 5 and 6), whereas on the other, taken along a dry run lined with sparse cottonwoods and willows, only 54% were eastern (cf. 14% western). This again suggests that western species are better represented in open country and open woodland habitats, and eastern species are better represented in rank or mixed woodland habitats (especially those with understory).

Along the Cimarron River, in southwestern Kansas, the eastern species are least well represented. However, in central Seward County there are more eastern individuals than in either Meade County to the east or Stevens County to the west (53% cf. 45% and 45%; see Fig. 5); correspondingly there are fewer western species in Seward County than in either Meade or Stevens counties (8% cf. 13% to 17%; see Fig. 6). This appears to be a reflection of an ecological "inversion" that exists along the Cimarron River: to both the east and west of the site studied in Seward County the Cimarron's flow is subterranean during much of the year, whereas in central Seward County there is always surface water. This not only guarantees a source of drinking water for animals, but also seems to permit a more luxuriant growth of vegetation. It is thought that the distribution of Baltimore and Bullock orioles, and of intermediates between them, is determined by environmental characteristics (probably including the presence of surface water) (Rising, 1970), and the "average phenotype" of female orioles from along the Cimarron similarly shows an inversion in Seward County (Fig. 8), although this is not true for males (Fig. 9).

Some of the southern species (Fig. 7) are found virtually throughout western Kansas, decreasing in density to the north; the Carolina Chickadee and Painted Bunting, however, are restricted to the Cimarron River and woodlands in the extreme south, and the Mississippi Kite and Bewick Wren are not found north of the Arkansas River Valley (Table 3). Several of these species appear to have extended their ranges northward within historic time (see Species Accounts beyond).

Unfortunately, census data on the grassland-scrub element are not available.

I calculated the faunal similarity among the 18 riparian localities in western Kansas listed in Table 3 using Jaccard's Coefficient of Association (Sokal and

[1] The numbers represent the numbers of singing males, or pairs, counted in censuses. These counts were made in riparian woodlands, usually over two days. The area censused varied, and estimates of the area (and hence of the density) were only approximate. The localities and days of census are indicated as follows: **1,** 8 mi E, 9 mi S Ashland, Clark County, 6-7 June 1965; **2,** 19 mi S, 2 mi W Meade, Meade County, 8-9 June 1965; **3,** 10 mi NNE Liberal, Seward County, 9 July 1965, 13-14 June 1966; **4,** 10 mi N, 8 mi W Hugoton, Stevens County, 9-10 June 1965, 5-7 June 1967; **5,** 7.5 mi N Elkhart, Morton County, 11-12 June 1965, 3-5 July 1966; **6,** 6 mi E Ford, Ford County, 2-5 June 1967; **7,** 9 mi W Dodge City, Ford County, 8 July 1965, 12 June 1966; **8,** 2 mi W Garden City, Finney County, 17 June 1965; **9,** 1 mi SE Coolidge, Hamilton County, 15-16 June 1965; **10,** 14 mi W, 18 mi S WaKeeney, Trego County, 21-22 June 1965; **11,** 18 mi N Scott City, Logan County, 25-26 June 1965, 17-20 June 1967; **12,** 2 mi N, 8 mi W Sharon Springs, Wallace County, 27-29 June 1965, 17 June 1967; **13,** 15 mi E, 15 mi S Hoxie, Sheridan County, 6-11 August 1966; **14,** 4 mi N, 1 mi E St. Francis, Cheyenne County, 14-16 June 1967; **15,** 7 mi SW St. Francis, Cheyenne County, 28 June, 6 July 1966; **16,** 15 mi N, 12 mi W St. Francis, Cheyenne County, 15 June 1967; **17,** "Dry Creek," 5 mi NE Atwood, Rawlins County, 11-12 June 1966; **18,** Beaver Creek, 5 mi NE Atwood, Rawlins County, 8-12 June 1966.

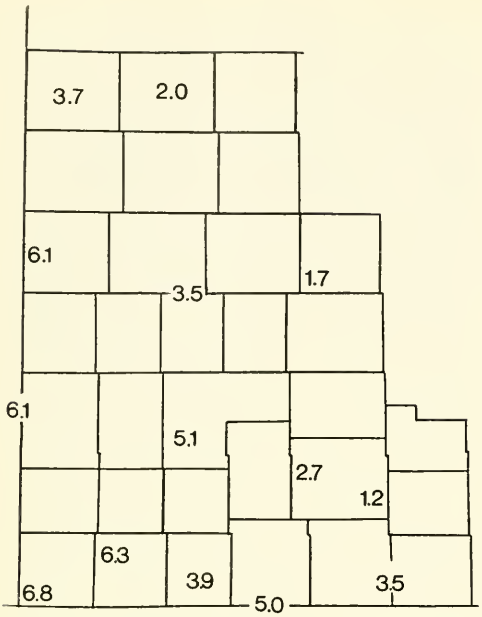

FIG. 8. Average character index scores of female orioles (*Icterus-galbula*, *I.-bullockii*, and intermediates) from 14 stations in western Kansas (from Rising, 1970). The values for individuals range from 0 to 7; 0 = *I.-galbula* and 7 = *I.-bullockii*.

Sneath, 1963: 133, 167). Figure 10 is a dendrogram illustrating the relationships thereby revealed which are based on the species composition (i.e., the presence or absence of species counted in my censuses at those sites, without consideration of their abundance). Even though such dendrograms most accurately illustrate the least inclusive clusters (groups or localities), but often distort the composition of the larger ones, the implied high avifaunal similarity between Ashland (Loc 1) and Liberal (Loc 3) relative to Meade (Loc 2), which is geographically between them along the Cimarron River, is consistent with the trend discussed above. The actual coefficient of similarity calculated between Locs 1 and 3 is 0.828; that between 1 and 2 is 0.567, and that between 2 and 3 is 0.677. The juxtaposition of Locs 1, 3, 4, 5, and 7 (Ashland, Liberal, Hugoton, Elkhart, and Dodge City) is probably a reflection of the "southern" birds censused at those stations. The wide separation of Loc 18 (the census taken in the mixed deciduous woods along Beaver Creek, near Atwood) reflects the species (primarily eastern woodland birds) that occur only there in our region. The dendrogram has many shortcomings, most conspicuously the lack of consideration of the interlocality variation in density of the species. Many of the commonest species, too, have no influence here because they are universally "present" (e.g., Western Kingbird, Baltimore/Bullock oriole).

Historical changes in the composition of the avifauna

It is apparent from the comparison of observations made in the past with those made today that the status of several species has changed greatly in the last 100 years (Table 4). Unfortunately, census

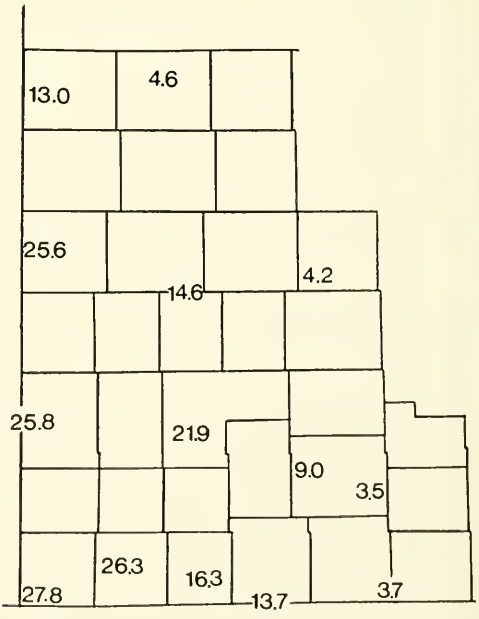

FIG. 9. Average character index scores of male orioles (*Icterus-galbula*, *I.-bullockii*, and intermediates) from 14 stations in western Kansas (from Rising, 1970). The values for individuals range from 0 to 29; 0 = *I.-galbula* and 29 = *I.-bullockii*.

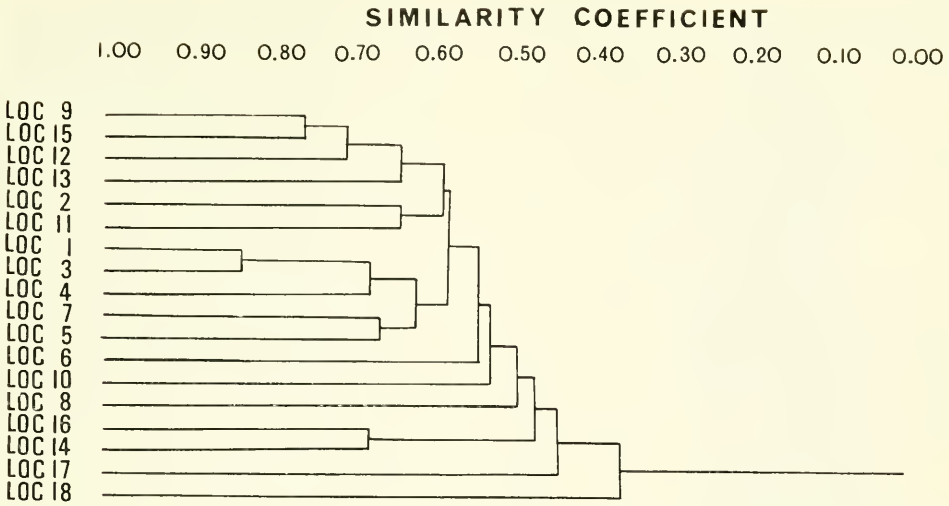

Fig. 10. Dendrogram showing comparison of 18 localities, based on Jaccard's Coefficient of Association, clustered by the unweighted pair-group method. Nonvariable characters (i.e., species present at all localities) were omitted from this analysis. For locality identification see footnote to Table 3.

data that could elucidate subtle changes are not available, although the information summarized in Table 3 may make such a comparison possible in the future. Of species whose ranges appear to be expanding into western Kansas (Table 4), about an equal number are expanding westward and eastward. The species moving eastward are forms that are characteristic of dry woodland ("red-shafted" flicker, Ladder-backed Woodpecker, Western Kingbird, Ash-throated Flycatcher, Black-billed Magpie, and perhaps Bullock Oriole), whereas those moving westward are divided between woodland (Mississippi Kite, Chuck-will's-widow, Red-bellied Woodpecker, Eastern Phoebe, Carolina Chickadee, Robin, Common Grackle, and Cardinal) and edge (Bobwhite, Eastern Meadowlark) species. Several of the latter, at least, have obviously benefited from development of "urban" habitats (Robin, grackle, Cardinal) as have the remaining "invading" species (Chimney Swift, Starling, House Sparrow).

On the other hand, most of the species "leaving" western Kansas are associated with grasslands (Greater and Lesser prairie chickens, Sharp-tailed Grouse, Mountain Plover, Upland Plover, Short-eared Owl, and Chestnut-collared Longspur) and it thus appears that modification of that sort of habitat has had a profound effect on the composition of the avifauna of western Kansas. Modification of the drainage of many of the watercourses may have reduced breeding populations of waterbirds (e.g. Yellow-headed Blackbird), but these must have been marginal populations in the first place.

Several species appear to be of cyclical occurrence in western Kansas. The Ladder-backed Woodpecker, Cassin Kingbird, Scissor-tailed Flycatcher, Rock Wren, Blue-gray Gnatcatcher, Indigo Bunting, Lazuli Bunting, and Lark Bunting are among these. Several (e.g., woodpecker, gnatcatcher, and Indigo Bunting) appear to be fairly common some years and absent others, whereas others (flycatcher, wren, and Lark Bunting) are always present, but during some years are notably

TABLE 4. Species showing changes in distribution in western Kansas in historical times.

Invading	Leaving
Mississippi Kite	Greater Prairie Chicken
Bobwhite	Lesser Prairie Chicken
Chuck-will's-widow	Sharp-tailed Grouse
Chimney Swift	Turkey
"red-shafted flicker"	Mountain Plover
Red-bellied Woodpecker	Upland Plover
Ladder-backed Woodpecker	Short-eared Owl
Western Kingbird	Black-capped Vireo
Ash-throated Flycatcher	Bell Vireo (?)
Eastern Phoebe	Yellow-headed Blackbird
Black-billed Magpie	Chestnut-collared Longspur
Carolina Chickadee	
Robin	
Starling	
House Sparrow	
Eastern Meadowlark	
Bullock Oriole (?)	
Common Grackle	
Cardinal	

widespread and abundant. These "cyclical species" are ecologically diverse.

Summary

The majority of the species of birds that breed (or probably breed) in western Kansas could be ecologically classified as "woodland," although the preponderance of such forms is less there than in the state of Kansas as a whole or in all of North America. This is doubtless a reflection of the rather poorly developed woodland habitat in western Kansas. The majority of the woodland species appear to have been derived from eastern North America.

On the other hand, the "grassland" avifauna is well developed, and the majority of the grassland species appear to have western affinities. It is the grassland element, however, that appears to have been most greatly affected by recent changes in the Plains' environment.

SPECIES ACCOUNTS

In the following section a paragraph is written about each species that is known to nest in western Kansas, or that has been seen there during the months of June and July. Where information is available, a brief indication of the species' status, its preferred habitat, and its distribution in western Kansas is given. Tree species are usually indicated only by a generic name; of these, *Populus* refers to *Populus-deltoides*, *Fraxinus* to *Fraxinus-pennsylvanica*, *Acer* to *Acer-negundo*, *Ulmus* to *Ulmus-pumila*, *Tamarix* to *Tamarix-gallica*, *Juniperus* to *Juniperus-virginiana*, *Prunus* to *Prunus-americana*, *Morus* to *Morus-alba*, *Maclura* to *Maclura-pomifera*, *Elaeagnus* to *Elaeagnus-angustifolia*, and locust to either *Gleditsia-triacanthos* or *Robinia-pseudoacacia*.

Information on nesting, taken from data at The University of Kansas Museum of Natural History, from the literature, and from my field notes, is summarized as follows: the number of eggs laid is given, as, for example, 3-4(3.5,3-4;4), which means that 3 and 4 are the commonest clutches, the average is 3.5 eggs, the range is 3 to 4, and the calculations of mode, mean, and range are based on 4 observations; the nest height is given as

4.0′ (2.5-7;6) high, which means that the average height is 4.0 ft., the range is 2.5-7 ft., and the calculations of mean and range are based on 6 observations. If only one or two records of clutch-size or nesting height are available, these are given without summary statistics. To indicate nest-site location, objects or plant species are listed in order of decreasing frequency with which they are used. For example the statement "Nests in a variety of trees (*Tamarix*, *Populus*, *Salix*, locust, *Juniperus*)" indicates that *Tamarix* (or *Tamarix* and *Populus* etc.) is most frequently used, and *Juniperus* is least frequently used. Specimens referred to are in the collection at The University of Kansas (Lawrence) ("KU") or at Ft. Hays Kansas State College (Hays) ("FHKSC"). Much distributional information for many species is summarized in Table 3.

Eared Grebe *Podiceps-caspicus*. One record: 1 mi N, 1.5 mi E Liberal, Seward County, 11 June 1963 (Zuvanich and McHenry, 1964).

Pied-billed Grebe *Podilymbus-podiceps*. Menke (1894) considered this a "common summer resident" in Finney County. A nest with 6 eggs was found near Garden City, Finney County, 9 July 1891, and Goss (1887) found three 1-2 day old chicks of this species at Crooked Creek, Meade County, 8 June 1886. I collected a Pied-billed Grebe (KU 54367) 15 mi E, 15 mi S Hoxie, Sheridan County, 8 August 1966, that may have been a transient.

Great Blue Heron *Ardea-herodias*. A common summer resident throughout, near water, in colonies, in tall trees (*Populus*) 40.0′ (20-50; 5) high; 2 (2.2, 2-3; 4) eggs are laid in April.

Green Heron *Butorides-virescens*. Local summer resident, near wooded ponds, except in extreme southwest. Wolfe (1961) considered them "a fairly common summer resident . . ." in Decatur County, but no nesting data are available.

Little Blue Heron *Florida-caerulea*. One record: a nest found 6 mi N, 4.5 mi W Garden City, Finney County, in 1952 (Tordoff, 1956).

Snowy Egret *Leucophoyx-thula*. Two nests found in 1952, 6 mi N, 4.5 mi W Garden City, Finney County (Tordoff, 1956), and one individual seen in Grant County, 11 June 1963 (Zuvanich and McHenry, 1964), appear to be the only records.

Black-crowned Night Heron *Nycticorax-nycticorax*. Low density local summer resident, near water. Linsdale (1927) found a nest with nearly grown young in a *Populus* at Coolidge, Hamilton County, 14 July 1921. Other summer records are from Gove, Kearny, Finney, Meade, Seward, Grant, and Stanton counties.

Yellow-crowned Night Heron *Nyctanassa-violacea*. Rare and local summer resident, near water. One record: pair building a nest, 40′ in *Populus*, Meade County State Lake, 7 June 1960.

Least Bittern *Ixobrychus-exilis*. Two sight records available: 3 mi E Lakin, Kearny County, 11 June 1955 (Mosby and Lynn, 1956); Atwood, Rawlins County, 27 June 1963 (Zuvanich and McHenry, 1964).

American Bittern *Botaurus-lentiginosus*. Rare and local summer resident, in marshes. Linsdale (1927) saw one near Coolidge, Hamilton County, 17 and 25 July 1921, and Menke (1894) considered the species a "common summer resident" in Finney County. A nest was found 6 mi N, 3.5 W Kalvesta, Finney County, in 1952 (Tordoff, 1956), and Imler (1936) mentions a nest found in Graham County (just east of the area covered by this report) in 1929.

White-faced Ibis *Plegadis-chihi*. One sight record: 9 mi N, 9 mi W Hugoton, Stevens County, 9 June 1965.

Canada Goose *Branta-canadensis*. Introduced as a summer bird in Cheyenne County, where it is said to breed occasionally.

Mallard *Anas-platyrhynchos*. Fairly common in summer, especially along Arkansas River, but only definite nesting records (2 nests) from Ford County (Mrs. A. R. Challans, *in litt.*).

Pintail *Anas-acuta*. Low density summer resident, found throughout, but especially from the Arkansas River Valley southward. Nesting records from Finney (3 records) and Meade counties.

Gadwall *Anas-strepera*. Low density summer resident, especially south of Arkansas River Valley. A female with 4 young seen at Cedar Bluff Reservoir, Trego County, 29 June 1963 (Zuvanich and McHenry, 1964), appears to be the only nesting record.

Green-winged Teal *Anas-carolinensis*. One summer sight record: a male seen at Kearny County State Lake, 8 June 1963 (Zuvanich and McHenry, 1964). The species is common in migration.

Blue-winged Teal *Anas-discors*. Fairly common local summer resident, in small ponds; most records from the Arkansas River Valley. Menke (1894) considered the Blue-winged Teal to be a "rare summer resident" in Finney County, and Wolfe (1961) writes: "A very rare summer resident; I found one nest with seven eggs on Johnson Draw, north of Oberlin [Decatur County], and another on Wild Cat Draw, southeast of Oberlin." These appear to be the only definite nesting records, although Goss (1885a) saw a pair at Wallace, Wallace County, 26 June 1884. The species is a common transient.

Cinnamon Teal *Anas-cyanoptera*. Probably a low density summer resident, in small ponds. Goss (1891) shot a female with a "well-developed ovary" in Meade County, 3 June 1885. Sight records are from Finney County (12 June) (Mosby and Lynn, 1956) and Gray County (10 June) (Zuvanich and McHenry, 1964).

American Widgeon *Mareca-americana*. Probably a low density summer resident, in small ponds. Goss (1891) saw a female near Wallace, Wallace County, 26 June 1884, that he thought probably had young. A recent sight record is from Meade County (14 June) (Mosby and Lynn, 1956). This widgeon is common in migration.

Shoveler *Spatula-clypeata*. Low density summer resident, in shallow ponds. Menke (1894) writes that the Shoveler occasionally bred in Finney County, and Goss (1885a) found six pairs near Ft. Wallace, Wallace County, 26 June 1884. No other breeding data are available for this species, common in migration.

Redhead *Aythya-americana*. A low density summer resident. Sight records are from Finney, Kearny, and Grant counties.

Lesser Scaup *Aythya-affinis*. One sight record: 1.5 mi S, 2 mi W Friend, Finney County, 12 June 1955 (Mosby and Lynn, 1956). The Lesser Scaup is a common migrant.

Ruddy Duck *Oxyura-jamaicensis*. Low density, local, summer resident. Recorded from Finney, Kearny, and Grant counties. Mosby and Lynn (1956) saw a female with six young, 6 mi W Ulysses, Grant County, 15 June 1955; no other nesting data are available.

Turkey Vulture *Cathartes-aura*. Moderately common throughout. Nests are placed on rock ledges; 2(1.7,1-2;3) eggs

are laid late April–late May. Nesting records are from Decatur and Trego counties.

Mississippi Kite *Ictinia-mississippiensis*. Common summer resident in riparian woodlands in the Arkansas and Cimarron river valleys; occasional, probably as a post-breeding wanderer, in Wallace and Cheyenne counties. This species appears to be expanding its range in Kansas. Menke (1894) does not mention it in his list of birds from Finney County, and Linsdale (1927) did not see them west of Sun City, Barber County, in 1921, although they were common along the Medicine River as early as 1887 (Goss, 1891). Fitch (1963) discusses their increase in density in Meade County which appears to have been correlated with increases in size and height of artificially established groves of trees there. Nests placed in trees (*Populus*, *Salix*, *Ulmus*, locust) 37.7′(24-50;7) high; 2(2.0,2;12) eggs are laid in early May. Nesting records are from Comanche, Meade (Fitch, 1963), Seward, Morton, and Ford counties.

Cooper Hawk *Accipiter-cooperii*. Low density, local summer resident in riparian woodlands. Wolfe (1961) found them to be "not uncommon" in Decatur County, and Menke (1894) called them "not common" in Finney County. I have two modern summer records: Coolidge, Hamilton County, 15 July 1964; Atwood, Rawlins County, 11 June 1966. Wolfe (1961) writes that he found "one or more nests . . . nearly every year" in Decatur County. Nesting began at the end of April there.

Red-tailed Hawk *Buteo-jamaicensis*. Low density summer resident, west to Stevens, Logan, Sheridan, and Rawlins counties. Wolfe (1961) considered it "very rare as a nesting species" in Decatur County. Nests are placed in trees (*Populus*, *Ulmus*, *Quercus*) 46.3′(20-70;4) high. Nesting records are from Comanche and Decatur counties.

Swainson Hawk *Buteo-swainsoni*. Common summer resident throughout, in open country. Nests placed in small stands or isolated trees (*Populus*, *Salix*, *Morus*) 29.6′(7-40;7) high; 3 (only record) eggs are laid mid-May–late May.

Ferruginous Hawk *Buteo-regalis*. Low density but regular summer resident in open country, at least in the central portion of western Kansas north to Cheyenne County. Nests are placed in small stands or isolated trees (*Populus*, *Morus*, *Maclura*), or on ledges 7-10′ high; 3(3.4,3-4; 5) eggs are laid early April–mid-April. Nesting records are from Wallace, Logan, Gove, Hamilton, and Finney counties.

Golden Eagle *Aquila-chrysaetos*. Probably a former or local summer resident, in open country. Goss (1891) thought that this species probably nested in Comanche County in the 1800s, but the only definite modern sight record is of a bird seen in Greeley County, 22 July 1959 (J. C. Barlow, pers. comm.). In the summer of 1921, Linsdale (1927) saw Golden Eagles at Coolidge, Hamilton County, on 12 and 17 July, and found a young bird, not able to fly, just west of there at Two Buttes, Prowers County, Colorado, 23 July. Ranchers in the bluff and badland regions of Comanche, Meade, Scott, and Logan counties frequently mention "eagle nests in caves"; however, these observations could possibly relate to *Cathartes-aura* or *Buteo-regalis*.

Marsh Hawk *Circus-cyaneus*. Low density or local summer resident in tall grassland, especially near water. Reported from all sectors. About nesting in Decatur County, Wolfe (1961) writes: "Nests were thick mats of grass and stems, placed on the ground, usually in late May."

Prairie Falcon *Falco-mexicanus*. Probably a local low density summer resident, near bluffs in open country. Linsdale (1927) saw single individuals north of Coolidge, Hamilton County, 17 and 27 July 1921; J. C. Barlow (pers. comm.) saw one at Point Rock, Morton County, 8 June 1960; I have seen them twice in western Kansas: 5 mi W Sharon Springs, Wallace County, 27 June 1965; 15 mi E, 15 mi S Hoxie, Sheridan County, 10 August 1966. In July 1965, J. A. Dick and I picked up the mummified carcass of a small (ca. 150 mm) downy *Falco* nestling, perhaps of this species, at the base of a "chalk bluff" in western Gove County. Unfortunately, the specimen was not saved.

Peregrine Falcon *Falco-peregrinus*. Perhaps a former local summer resident. J. A. Allen (1872a) found a nest containing half-grown young on a cliff overlooking the Saline River in Ellis County, 29 May 1871, just east of the region covered by this report.

Sparrow Hawk *Falco-sparverius*. Common summer resident along roadsides and riparian woodlands throughout. Nests in hollow trees (commonly solitary dead *Populus*).

Greater Prairie Chicken *Tympanuchus-cupido*. Apparently a fairly common resident in the northwest for a brief period of time. Allen (1872a) says that the species was first reported in the vicinity of Ft. Hays in Ellis County (just east of the region covered by this report) in about 1869. It apparently was fairly common there until the turn of the century, and persisted until the mid-1920s (Ely, 1971). Of this species' status in Decatur County, Wolfe (1961) writes: "Very common over the entire county in the early days, but rare by 1914. The birds nested in thick bunch grass, about the middle of May."

Lesser Prairie Chicken *Tympanuchus-pallidicinctus*. Found north and east to Hamilton (Graber and Graber, 1951; Clifford Low, at Coolidge, pers. comm.) and Ford counties. Prairie chickens reported by Menke (1894) in Finney County, where they were "abundant," and by Linsdale (1927) from Gove and Kearny counties were probably this species. The Lesser Prairie Chicken is at least moderately common in Meade and Morton counties. A hen with 10 young was seen near Dodge City, Ford County, 1 June 1955 (Johnston, 1964).

Sharp-tailed Grouse *Pedioecetes-phasianellus*. Former resident. Allen (1872a) found this species commonly in Ellis County (just east of the region covered herein) in 1871; however, Ely (1971) mentions that it had disappeared from that county by 1875, apparently being replaced by *Tympanuchus-cupido*.

Bobwhite *Colinus-virginianus*. A common resident throughout, in brushy edges. In pre-agricultural times this species may have been restricted to the far west. Elliott Coues (*fide* Goss, 1891) collected two females on the Republican River in northwestern Kansas (Cheyenne County), 27 May 1864, and Goss (1891) also mentions that they were ". . . occasionally seen on the Cimarron River, south of Ft. Dodge [probably in Clark County], from 1862 to 1866" by army hunters, and Goss believes that this was before the "eastern" Bobwhite, following settlement, had made it beyond central Kansas. Allen (1872a) writes that in Ellis County they were "occasional, but every year . . . becoming more common . . . working westward, following the settlers," and Menke (1894) writes that they were "comparatively abundant since the introduction of six dozen in 1891" in Finney County. Nests are placed on the ground, in "buffalo

grass" and other vegetation; 11-12 eggs are laid late May–mid-July.

Scaled Quail *Callipepla-squamata*. A moderately common resident in xeric scrub, from Hamilton south to Meade and Morton counties. Nests are presumably placed on the ground, probably near *Opuntia* or *Artemisia*; 10 eggs (only record) are laid mid-June–late July. Nesting records are from Hamilton and Morton counties.

Ring-necked Pheasant *Phasianus-colchicus*. Common resident throughout, in open country. Lowest density along the Cimarron River in the southwest. Introduced into western Kansas after the turn of the present century. Nests placed on the ground, in rank brush; 6-7 eggs are laid early May–mid-June.

Turkey *Meleagris-gallopavo*. Perhaps formerly occurred in western Kansas; Allen (1872a) found them common near Ft. Hays, Ellis County, in 1871, although they were probably extirpated there late in the 19th century (Ely, 1971). Today, following introduction into Oklahoma, they are fairly common along the Cimarron River at least as far west as Hugoton, Stevens County, where I saw one 5 June 1967, and Elkhart, Morton County, where a nest was found 13 May 1967 (Ely and Thompson, 1971). They have also been introduced locally in Logan County, where a small flock persists and is probably dependent upon artificial feeding during the winter (C. Hardin, pers. comm.). Nests are placed on the ground; 9-13 (11.3,9-13; 3) eggs are laid in May. Records of nesting are from Comanche (Rising, 1965a), Morton, and Logan counties.

King Rail *Rallus-elegans*. Possible summer resident in Meade County (Johnston, 1964).

Virginia Rail *Rallus-limicola*. Doubtless an irregular, low density summer resident. Menke (1894) said that they were a "common summer resident in rainy seasons" in Finney County; Graber and Graber (1951) found an adult with a brood of six young, 8 mi S Richfield, Morton County, 23 May 1950.

Sora *Porzana-carolina*. Menke (1894) considered the Sora a "rare summer resident" in Finney County, and there is no other indication that this species occurs in the summer in western Kansas.

Black Rail *Laterallus-jamaicensis*. Probably a rare and irregular summer resident. G. G. Menke found a nest with nine eggs, Finney County, 6 June 1889, and there is a nesting record from Meade County (Johnston, 1964).

Common Gallinule *Gallinula-chloropus*. One record: specimen taken near Hackberry Creek, Gove County, 14 June 1878 (Goss, 1886).

American Coot *Fulica-americana*. Probably locally common as a summer resident. Menke (1894) considered the coot to be a "common summer resident" in Finney County, and Goss (1885a) found four pairs near Ft. Wallace, Wallace County, 26 June 1884. Modern sight records are available from virtually throughout western Kansas (Mosby and Lynn, 1956; Zuvanich and McHenry, 1964). I found two pairs, each with two-thirds-grown young, in small ponds 7.5 mi N, 4 mi E Elkhart, Morton County, 21 June 1967.

Snowy Plover *Charadrius-alexandrinus*. Low density, local summer resident, on sand bars. Nests are apparently placed on the sand; 3(3.0,3;4) eggs are laid late May–early June. Actual nesting records are from Comanche and Finney counties, but specimens taken during the nesting season and sight records from that season

are from Clark, Meade, and Scott counties also.

Killdeer *Charadrius-vociferus*. Moderately common summer resident throughout, especially in river valleys. Nests are placed on the ground; 3 (only record) eggs are laid in May and June.

Mountain Plover *Eupoda-montana*. Formerly apparently fairly common as a summer resident, but much reduced or absent today. Allen (1872a) found this species to be "moderately common" in Ellis County in 1871, and Menke (1894) considered it an "abundant summer resident" in Finney County before the turn of the century. As far north as Decatur County, Wolfe (1961) recalls that the Mountain Plover was a "very rare summer resident found only in areas of short buffalo grass on open plains." In June of 1911 Bunker and Rockland obtained six specimens of this species in Greeley and Haskell counties (KU 5509, 5511-15), including two chicks from Greeley County (KU 5512-13) on 21 June 1911. Flocks seen in Hamilton County, 27 July 1921 (Linsdale, 1927) and 15-16 July 1964 (Rising and Kilgore, 1964), may indicate that nesting occurs in that area. About nesting, Wolfe (1961) writes: "The nest was a slight depression in the ground lined with a few grass stems. The number of eggs was usually three, laid in the last of May."

Long-billed Curlew *Numenius-americanus*. Low density summer resident in high plains. Schwilling (1956) reports a nest containing 4 eggs from Stanton County, and there are specimens of two "local" birds (KU 16608-9) taken 27 June 1927 in Morton County. Sight records are from Morton, Stanton, Meade, and Stevens counties.

Upland Plover *Bartramia-longicauda*. Uncommon, local summer resident, in mature grassland. Modern records are from the southwestern sector (Morton, Stanton, Meade, Comanche, Edwards, Ford, Kearny, and Trego counties). This species was apparently formerly more common. Of its status in Decatur County, Wolfe (1961) writes: "This species was not uncommon in the early years but was not seen after about 1910." Menke (1894) considered it a "common summer resident" in Finney County, and Linsdale (1927) collected a young female south of Coolidge, Hamilton County, 13 July 1921. Of nesting Wolfe (1961) writes: "The nest was well concealed in thick grass. . . ."

Spotted Sandpiper *Actitis-macularia*. Probably a low density summer resident in riparian situations. Recorded rather frequently during June and July (Comanche, Seward, Morton, Ford, Decatur, Cheyenne counties). The species is common in migration.

Greater Yellowlegs *Totanus-melanoleucus*. One sight record: Decatur County State Lake, 27 June 1963 (Zuvanich and McHenry, 1964). The species is common in migration.

Lesser Yellowlegs *Totanus-flavipes*. Two records: Decatur County State Lake, 27 June 1963 (Zuvanich and McHenry, 1964); 4 mi N Coolidge, Hamilton County, 16 July 1964. The species is common in migration.

Baird Sandpiper *Erolia-bairdii*. One sight record: Sheridan County State Lake, 27 June 1963 (Zuvanich and McHenry, 1964). The species is common in migration.

Long-billed Dowitcher *Limnodromus-scolopaceus*. One sight record: Cedar Bluff Reservoir, Trego County, 29 June 1963 (Zuvanich and McHenry, 1964). The species is common in migration.

American Avocet *Recurvirostra-americana*. Locally common summer resident, in shallow prairie ponds. Nests placed on mud near shallow lakes; 4(3.9,3-4;11) eggs are laid in the latter two-thirds of May. Nesting records are from Finney and Meade (one instance) counties; recorded also from Stevens, Seward, Grant, and Hamilton counties.

Black-necked Stilt *Himantopus-mexicanus*. Menke (1894) took a specimen in Finney County, 16 May 1892, and saw 6 there, 13 June 1892. A specimen was taken near Lakin, Kearny County, in mid-June 1881 (Goss, 1886). Two modern sight records: 1 mi NE Liberal, Seward County, 15 June 1955 (Mosby and Lynn, 1956); 0.5 mi N Tennis, Finney County, 9 June 1963 (Zuvanich and McHenry, 1964). The species is perhaps a low density summer resident.

Wilson Phalarope *Steganopus-tricolor*. Low density summer resident, in shallow ponds. Records are from Finney, Kearny, Meade, and Seward counties. Goss (1887) found this species nesting along Crooked Creek, Meade County, 8 June 1886. Nests placed on ground near water; 4(3.7,3-4;3) eggs are laid in early June.

Ring-billed Gull *Larus-delawarensis*. One sight record: 4 at Kearny County State Lake, 8 June 1963 (Zuvanich and McHenry, 1964). The species is common in migration.

Franklin Gull *Larus-pipixcan*. One sight record: 4 at Kearny County State Lake, 8 June 1963 (Zuvanich and McHenry, 1964). The species is common in migration.

Forster Tern *Sterna-forsteri*. Two sight records: 3 mi E, 6 mi N Garden City, Finney County, 12 June 1955 (Mosby and Lynn, 1956); 12 seen Kearny County State Lake, 8 June 1960 (J. C. Barlow, pers. comm.).

Least Tern *Sterna-albifrons*. Local summer resident, near water (especially sand bars in rivers). Nests placed on sand; 3 (only record) eggs are laid mid-June–late June. Nesting records are from Finney, Trego, Meade, and Hamilton counties; also reported from Comanche County in summer.

Black Tern *Chlidonias-niger*. Low density, local summer resident, near small ponds with emergent vegetation. Eggs probably laid in May, as immature birds seen in Finney and Seward counties (Zuvanich and McHenry, 1964) in mid-June. Reported from Finney, Seward, and Meade counties.

Rock Dove *Columba-livia*. Fairly common resident throughout, about habitations or natural ledges. Nests placed under bridges, on ledges 7.3′ (5-12;7) high; 2(1.8,1-2;5) eggs are laid May and June.

Mourning Dove *Zenaidura-macroura*. Abundant summer resident throughout, in open woodlands and open country. Nests placed on ground (8.8%) or in a variety of trees (*Populus*, *Salix*, *Tamarix*, *Acer*, *Ulmus*, *Juniperus*, *Morus*, *Vitus*, *Fraxinus*, locust, exotic conifers), 10.8′ (2.5-30;53) high; 2(2.0,2;41) eggs are laid mid-March–mid-July (Fig. 11), with a peak in May and June.

Yellow-billed Cuckoo *Coccyzus-americanus*. Common summer resident throughout, in rank riparian thickets (*Salix-Morus-Populus*). Nests placed in low perennial vegetation (*Salix*, *Populus*, *Acer*, *Prunus*), 12.7′ (4-30;4) high; 4(3.8,3-4;5) eggs are laid early June–mid-July (Fig. 12).

Black-billed Cuckoo *Coccyzus-erythropthalmus*. Locally common, and probably irregular summer resident in the same

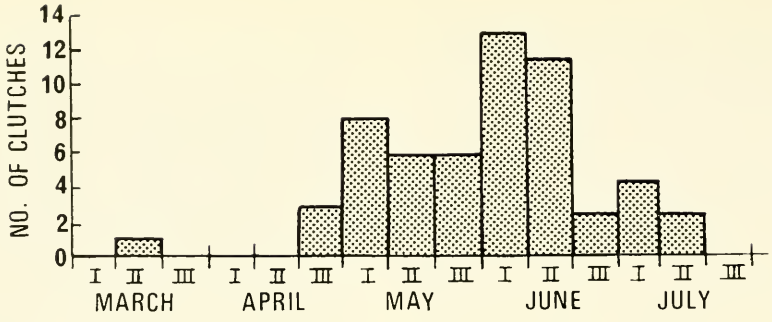

FIG. 11. Histogram of the breeding schedule of the Mourning Dove in western Kansas. The height of the columns indicates the number of clutches completed in the 10-day intervals indicated by the width of the columns.

habitat as the previous species. Nests contain 4 eggs (only record), and are complete mid-June and early July (two records: Seward and Cheyenne counties).

Roadrunner *Geococcyx-californianus*. Perhaps a low density summer resident. Two records are from the winter: a female (KU 33563) taken 1 mi N, 10 mi E Coldwater, Comanche County, 9 January 1957; a male (KU 20904) taken 1 mi E Arkalon, Seward County, 6 November 1934.

Barn Owl *Tyto-alba*. Moderate density summer resident throughout, in riparian woodlands or badlands. Nests placed on cliffs or in trees, 12-20′ high; 5 eggs (only record) are laid late April–late May.

Screech Owl *Otus-asio*. Moderate density resident throughout, in riparian woodlands. Marshall (1967) has reexamined the screech owls of North America, and specimens of this species from Kansas. He concluded that all of the individuals from Kansas (including Linsdale's [1927] specimen [KU 20886] collected at Coolidge, Hamilton County, 17 July 1921, which has been called apparently inappropriately "*Otus-asio aikeni*") are "eastern" Screech Owls (*Otus-asio*, cf. *Otus-kennicottii*). *Otus-asio* has been taken west to Rawlins (KU 53059-60), Hamilton, Morton, Ford (KU 57741), and Seward counties, and *Otus-kennicottii* (*sensu* Marshall) east to Cimarron County, Oklahoma, and Otero County, Colorado (Marshall, 1967). Nests placed in cavities in trees, 3-12′ high; 4 eggs (only record) are laid in early April in Decatur and Rawlins counties.

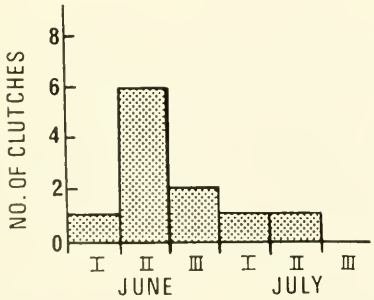

FIG. 12. Histogram of the breeding schedule of the Yellow-billed Cuckoo in western Kansas. For explanation, see caption to Figure 11.

Great Horned Owl *Bubo-virginianus*. Common resident throughout, in woodlands and canyons. Nests placed in large trees (*Populus*), on cliff faces, and on ledges, 25.1′ (14-45;8) high; 2(2.4.2-3;5) eggs are laid mid-February–mid-March.

Burrowing Owl *Speotyto-cunicularia*. Common summer resident, in open pasture and roadsides; often associated with prairie dog villages. Nests placed in burrows in the ground; 7-8 eggs are laid in May.

Barred Owl *Strix-varia*. One sight record:

in rank riparian woodlands, 5 mi W Dodge City, Ford County, 8 July 1965.

Long-eared Owl *Asio-otus*. Probably a low density local resident in woodlands. Wolfe (1961) writes: "An irregular summer resident. In some years two or three nests with eggs or young could be found [in Decatur County] and then the birds would not be seen again for a year or more." Menke (1894) calls the species "Common" without any other qualification, in Finney County, and Johnston (1964) mentions nesting records from Trego and Meade counties. The species has doubtless suffered greatly from depredation by European man.

Short-eared Owl *Asio-flammeus*. Perhaps a low density local resident, in rank grasslands and marshy areas. Wolfe (1961) writes: "A rare summer resident [in Decatur County]. These owls were found only on open prairie thickly covered with bunch grass or bluestems; the nest was a depression in the ground under thick grass." Menke (1894) called it a "Plentiful resident" in Finney County, and Linsdale (1927) saw the species in Gove County, 27 July 1921. Habitat suitable for Short-eared Owl nesting has doubtless been greatly reduced with the clearing of the prairies, and the species may no longer breed in the western portion of the state, although J. C. Barlow (pers. comm.) saw one in Greeley County, 22 July 1959.

Chuck-will's-widow *Caprimulgus-carolinensis*. Local summer resident in Edwards and Comanche counties, in rank woodlands. The Chuck-will's-widow appears to be rapidly expanding its range westward in Kansas (Shane, 1966). I heard at least three individuals calling and took one specimen (KU 49243) from rank riparian brush, 8 mi S, 9 mi E Ashland, Clark County, 6 June 1965. S. A. Rohwer, D. M. Niles, and I heard two others and obtained one specimen (KU 61551) 2 mi S Kinsley, Edwards County, 10 May 1968; the specimen was a first year female with one shelled egg in her oviduct and one yolked ovum enlarged to 18 mm.

Whip-poor-will *Caprimulgus-vociferus*. In his list of the birds of Finney County compiled in the late 1800s, Menke (1894) writes: "Rare summer visitant. Two specimens." I have not seen these specimens, nor do I know the whereabouts of them.

Poor-will *Phalaenoptilus-nuttallii*. Uncommon or local summer resident, near bluffs and canyons. Records are from Morton (Graber and Graber, 1951) and Comanche (12 May 1968) counties. Imler (1936) mentions a specimen taken 20 July 1929 in Ellis County, east of the region covered by this report.

Common Nighthawk *Chordeiles-minor*. A common summer resident throughout. Nests are placed on the ground; 2 eggs (only record) are laid in early June.

Chimney Swift *Chaetura-pelagica*. Local summer resident about urban areas, found west to Morton, Hamilton, Scott (Rising 1965a) and Cheyenne counties. No nesting data are available.

Ruby-throated Hummingbird *Archilochus-colubris*. Probably a low density transient (Imler, 1936; Menke, 1894). I saw a female or juvenile 15 mi E, 15 mi S Hoxie, Sheridan County, 8 August 1966, that may have been *Archilochus-alexandri*.

Belted Kingfisher *Megaceryle-alcyon*. Summer resident throughout in riparian situations. No nesting data are available.

Yellow-shafted/Red-shafted Flicker *Colaptes-auratus*. Common summer resident throughout; highest densities along Arkansas and Republican river systems. At

eastern edge most individuals are of the "yellow-shafted" morph; however, especially in Cheyenne and Rawlins counties, individuals intermediate between "red-" and "yellow-shafted" morphs are numerous. Along the Cimarron River such intermediate individuals are rare, and pure "red-shafted" individuals are common west of Folsom, Union County, New Mexico, and occur in low density in Morton County, Kansas. Wolfe (1961) mentions only the yellow-shafted flickers from Decatur County, implying that red-shafted individuals were rare there (at least at the turn of the century). Short (1965) has discussed the Plains *Colaptes* in detail. Nests are placed in cavities in large (often dead) branches of trees (*Populus*, *Fraxinus*), 19.2′ (5-35;9) high; (5.0,5;10) eggs are laid late April–mid-June (Fig. 13).

Red-bellied Woodpecker *Centurus-carolinus*. Uncommon and local resident in Comanche, Rawlins, Decatur, and Hamilton counties. Wolfe (1961) does not mention this species as among those he found in Decatur County at the turn of the century, but I found several there in February 1967, suggesting that this species is extending its range westward. Schwilling (1954) saw the species in Morton County, 27 September 1954. Imler (1936) saw them in Rooks County (east of the region covered in this report) in 1932-33 and 1936. A female (KU 53068) collected in *Fraxinus-Morus* woodlands, 5 mi NE Atwood, Rawlins County, 12 June 1966, had enlarged follicles and a defeathering brood patch. A female was flushed from a nest cavity 5 mi W Syracuse, Hamilton County, 28 April 1967 (Ely and Thompson, 1971).

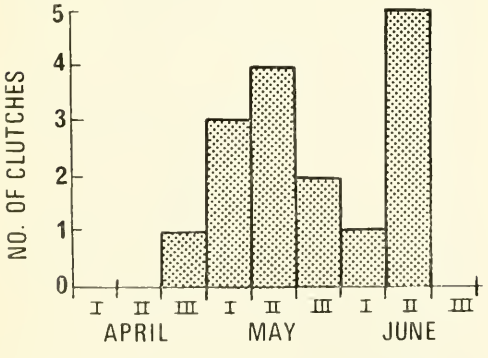

FIG. 13. Histogram of the breeding schedule of flickers ("red-shafted," "yellow-shafted," hybrids) in western Kansas. For explanation, see caption to Figure 11.

Red-headed Woodpecker *Melanerpes-erythrocephalus*. Common summer resident throughout, in open woodlands. Nests placed in trees (*Salix*, *Populus*, *Ulmus*), 3-12′ high; 4-6(5.0,4-6;3) eggs are laid in June.

Lewis Woodpecker *Asyndesmus-lewis*. One record: one seen 2 mi N Holcomb, Finney County, 6 June 1955 (Schwilling, 1956).

Hairy Woodpecker *Dendrocopos-villosus*. Low density resident throughout, in woodlands. Nests placed 10-20′ high, in tree trunks (*Populus*, *Fraxinus*); 4 (only record) eggs are laid mid-April–early May. Nesting records are from Decatur, Seward, and Comanche counties.

Downy Woodpecker *Dendrocopos-pubescens*. Moderate density resident throughout, in woodlands. Nests in trees; 5(4.7, 4-5;3) eggs are laid mid-April–early May. Nesting records are from Seward County.

Ladder-backed Woodpecker *Dendrocopos-scalaris*. Low density and probably eruptive resident in southwest, in woodlands along Cimarron and Arkansas rivers. The Grabers (1950) found Ladder-backed Woodpeckers to be fairly common in *Populus* woodlands along the Cimarron River in Morton County in 1950 when they collected 5 specimens (26 February–9 May). The species was not subsequently reported from the state, in spite of much field work in the mid-1960s in the south-

west, until a female with a brood patch was collected (FHKSC 1399) 5 mi W Syracuse, Hamilton County, 28 April 1967 (Ely and Thompson, 1971). A male (FHKSC 1445, testes 8 × 4 mm) was collected 9 mi N, 4.5 mi E Elkhart, Morton County, 12 May 1967, and another male was flushed from a nest cavity ca. 3 ft. from the ground in a small *Populus* at the latter locality 3 June 1968 (Ely and Thompson, 1971). J. A. Jackson and I saw a male at the Morton County locality 21 June 1968, perhaps the same as the aforementioned bird.

Eastern Kingbird *Tyrannus-tyrannus*. Common summer resident throughout, in isolated trees or at the edge of woodlands. Although this species may be found any place the Western Kingbird is, it nonetheless shows a preference for riparian trees, and commonly nests in willows over or near water (Table 5). Along the Republican River in northwestern Kansas the Eastern is the most common kingbird; it is relatively uncommon along dry stretches of the Cimarron River in the extreme southwestern corner of the state where surface water is not always available, and in general is less common than *T.-verticalis* in western Kansas. *T.-tyrannus* arrives in western Kansas somewhat later than *T.-verticalis*, and is not common until mid-May. Nests are placed 10-30′ high in a variety of trees, but primarily *Populus* and *Salix* (Table 5); the 4 eggs (2 records) are laid late May–early July (peak early June; later clutches may be replacement nests). Occasionally parasitized by cowbirds (Friedmann, 1934).

Western Kingbird *Tyrannus-verticalis*. Common throughout, in isolated trees or at the edge of woodlands. The Western and Eastern kingbirds overlap extensively in habitat preferences, but this is the conspicuous form about isolated ranch houses, in towns, on windmills, and in other nonriparian situations, and is the commonest tyrannid in western Kansas at most localities. Nests are placed 8-50′ high in a variety of trees, but primarily *Populus* and *Ulmus* (Table 5); 4-5(4.4,3-5;11) eggs are laid mid-May–mid-July (peak mid-June).

The Western Kingbird may formerly have been less common than today. Menke (1894) does not mention it in his list of birds compiled in the early 1890s from the vicinity of Garden City, Finney County, nor does Tiemeier (1942) mention it as among the species found near Ludell, Rawlins County, 27 July–1 August 1936. However, Wolfe (1961) records *T.-verticalis* as abundant, ". . . equal in numbers to the Eastern Kingbird . . ." in Decatur County 1908-1915 (as they are today), Imler (1936) found them abundant in Rooks County (east of the region covered in this report) in the 1930s, and Linsdale (1927) found them "common" in Pratt, Finney, Kearny, Hamilton, and Gove counties in 1921.

Cassin Kingbird *Tyrannus-vociferans*. Perhaps breeds locally or sporadically in western Kansas. The only spring or sum-

Table 5. Comparison of site and elevation of nest-sites used by kingbirds in western Kansas.

Species	Cottonwood	Willow	Chinese Elm	Other[1]
Eastern Kingbird	21.7,20-25;3[2]	17.7,10-30;4	.....	16.0,15-17;2
Western Kingbird	35.3,11-65;32	.....	22.6,8-50;9	23.0,15-30;5
Scissor-tailed Flycatcher	20.0,5-35;3	.....	16.0,15-17;2	10

[1] Includes ash, oak, mulberry, box elder, dead trees, and fence and telephone poles.
[2] The mean = 21.7 feet, the range = 20-25 feet, and the sample size = 3.

mer records are those of Graber and Graber (1950) who saw as many as two pairs along the Cimarron River north of Elkhart, Morton County, 14-26 May 1950, and collected a male ("testes much enlarged") there on 26 May. This species is fairly common at higher elevations along the Cimarron River near Folsom, Union County, New Mexico.

Scissor-tailed Flycatcher *Muscivora-forficata*. Common in central and south-central Kansas west to Stevens County along the Cimarron River, to Finney County along the Arkansas River, and to Sheridan County along the Saline River; breeds in low density in Morton County and probably in Kearny County. In western Kansas maximal densities are reached in Comanche County west to Meade, where *M.-forficata* is common along the Cimarron and Salt Fork rivers and smaller watercourses as well as in shelter-belts and near human habitations. This species seems to show considerable fluctuation in numbers especially at the periphery of its range. For example, they were fairly common along the Cimarron River north of Elkhart, Morton County, in 1963 and 1964, but scarce there in 1965, 1966, and 1967. Nests are placed 10-20′ high in trees (*Populus*, *Ulmus*), crossbars on telegraph poles, or in the structure of windmills (Table 5); 3-4(3.5,3-4;4) eggs are laid late-May–mid-July (peak mid-June).

Great Crested Flycatcher *Myiarchus-crinitus*. Present in riparian cottonwoods throughout, except in Morton County. Highest densities are in Comanche and Clark counties, and density decreases toward the western part of the state at all latitudes. Nests are placed in cavities in *Populus*, perhaps 15′ high (only record); 6(6.3,5-8;4) eggs are laid late May–mid-July.

Ash-throated Flycatcher *Myiarchus-cinerascens*. Doubtless breeds in low density along the Cimarron River in extreme southwest. Graber and Graber (1950) found them to be fairly common and apparently nesting in cottonwoods along the Cimarron in May 1950; they collected a female ("ovary somewhat enlarged") there on 5 May. Four other specimens from along the Cimarron River in Morton County may well have been breeding birds: KU 41627, taken 17 July 1963 (testis = 8 mm, a little fat); KU 45566, taken 12 July 1964 (testis 11 × 5 mm, little fat) (Rising and Kilgore, 1964); FHKSC 603, taken 4 May 1963 (testis 8 mm, some fat); and FHKSC 1395, taken 29 April 1967 (ovary 10 × 5 mm, little fat) (Ely and Thompson, 1971). A male (KU 49250) with testis enlarged (10 × 6 mm) was taken 8 June 1965, 19 mi S, 2 mi W Meade, Meade County, from a planted stand of open cottonwoods near the Cimarron River (Rising, 1965a); at that locality this species is sympatric with *M.-crinitus*.

Eastern Phoebe *Sayornis-phoebe*. An uncommon or local summer resident in the eastern portions of the region covered by this report. I have collected apparently paired birds from canyons in Comanche County in April, and would assume that they breed there. Adults and newly fledged young were collected from near a bridge over the Smoky Hill River, 14 mi W, 18 mi S WaKeeney, Trego County, 22 June 1965; the birds may have nested beneath the bridge or in nearby rocky bluffs. I have also seen Eastern Phoebes along Sappa Creek, 2 mi E, 1 mi N Oberlin, Decatur County (27 July 1963), along Beaver Creek, 2 mi NE Ludell, Rawlins County (June 1966), and near the Republican River, 7 mi SW St. Francis, Cheyenne County (28 June 1965). Graber and Graber (1951) saw a single Eastern

Phoebe near Syracuse, Hamilton County (17 April 1950). Wolfe (1961) and Tiemeier (1942) did not find this species in either Decatur or Rawlins counties, respectively, earlier in the century, suggesting a possible expansion of range into northwestern Kansas.

Say Phoebe *Sayornis-saya*. A locally common summer resident, near rocky Cretaceous chalk bluff or about abandoned buildings. Nests are placed in culverts or bridges (3 records), in abandoned houses (2 records), or in niches in cliffs (1 record). Wolfe (1961) mentions that Say Phoebes nested commonly in abandoned wells in Decatur County at the turn of the century; 5(4.8,3-6;5) eggs are laid late May–mid-July. Cowbird parasitism appears to be common (Friedmann, 1963). Nesting records from Decatur, Hamilton, Johnson, Logan, and Trego counties, and probably from Gove County (Linsdale, 1927).

[*Empidonax* Flycatchers. *E-flaviventris*, *E.-traillii* (*s.l.*), *E.-minimus*, *E.-wrighti*, *E.-oberholseri*, *E.-hammondii*, and *E.-difficilis* all occur in migration, but none is known to nest. *E.-traillii*, *E.-minimus*, and *E.-oberholseri*, however, have all been recorded during the summer and may breed in western Kansas.]

Traill Flycatcher *Empidonax-traillii* (*s.l.*). A common transient in riparian *Populus-Salix* growth. In the spring specimens have been taken 12-24 May, and in the fall 7-29 August; all specimens examined are of adult birds, so first-year individuals probably migrate later in the fall. Two specimens (KU 49245, taken 8 June 1965 in Beaver County, Oklahoma, 21 mi S Meade, Kansas [Rising, 1965a], and KU 53177, taken 3 July 1966, 7.5 mi N, 2 mi E Elkhart, Morton County) are of adult males that may have been on breeding territories; neither was singing.

Least Flycatcher *Empidonax-minimus*. A common transient in riparian arboreal vegetation. In the spring Least Flycatchers are common late April–mid-May; fall specimens are from 25 July-11 August (all adult birds; first-year birds doubtless migrate later). One specimen (KU 49147, an adult female taken 15 mi N, 12 mi W St. Francis, Cheyenne County, 6 July 1965) was probably a migrant.

Dusky Flycatcher *Empidonax-oberholseri*. Specimens of the Dusky Flycatcher are 29 April-13 May (Morton, Seward, and Finney counties) (Ely and Thompson, 1971). One other specimen (KU 49246, an adult female taken 14 mi W, 18 mi S Wa-Keeney, Trego County, 22 June 1965) was doubtless a transient (Rising, 1965b).

Wood Pewee *Contopus-virens* and *Contopus-sordidulus*. Local or irregular low density summer resident, in woodlands. Barlow and Rising (1965) discussed the identification of several *Contopus* specimens from along the Cimarron River in Stevens and Morton counties, and their status there; they suggested that *C.-virens* and *C.-sordidulus* may hybridize in that region, and Short (1961) similarly suggested that hybridization may occur in western Nebraska. After the preparation of the 1965 paper, I collected an adult male *Contopus* from along the Cimarron River north of Elkhart, Morton County (KU 49249, 11 June 1965), that sang the primary song characteristic of *C.-virens* and whose plumage features were like *C.-virens*. This individual had testes enlarged (9 × 5 mm), was seemingly territorial, but may not have been paired (Rising, 1965a). Another individual (KU 49248), also a male (testis 3 × 2 mm), was taken 27 June 1965, 2 mi N Sharon Springs, Wallace County. This latter individual was not singing, and is intermediate in plumage features between *C.-*

virens and *C.-sordidulus* (Rising, 1965a). On 6-7 June 1967 I collected four (KU 57751-4; KU 57751-3 are females) additional *Contopus* from along the Cimarron River near Hugoton, in Stevens County. One of these birds (KU 57754) sang the song of *C.-sordidulus*, and all appear to be *C.-sordidulus*. Ely and Thompson (1971) also mention five specimens from Morton County.

It is probable that both *C.-virens* and *C.-sordidulus*, as presently understood, breed in low density in western Kansas, perhaps in greatest density along the Cimarron River in the southwest. However, some of the individuals taken, especially those taken in early June, may well be late migrants.

Olive-sided Flycatcher *Nuttallornis-borealis*. According to Goss (1891) a pair of Olive-sided Flycatchers nested near the top of a large solitary *Populus* near Wallace, Wallace County, 27 May 1883. This record has apparently been rejected by other workers, and indeed the date seems early for nesting by this species, but it is difficult for me to discount completely an observation from such an experienced observer as Goss who was quite familiar with this and other *Contopus*.

Horned Lark *Eremophila-alpestris*. An abundant resident throughout, in short-grass prairie and pastures. Nest placed on ground, in open; 3(3.3,3-4;3) eggs are laid early March–early May (peak March-April [Fig. 14]).

Bank Swallow *Riparia-riparia*. Probably a local summer resident. In the summer of 1936, Tiemeier (1942) saw this species "commonly" along the banks of Beaver Creek, Rawlins County, but Wolfe (1961) found only a few small colonies at Oberlin, Decatur County, in the early 1900s, and considered them a "rare summer resident" there. I have not seen Bank Swallows in western Kansas.

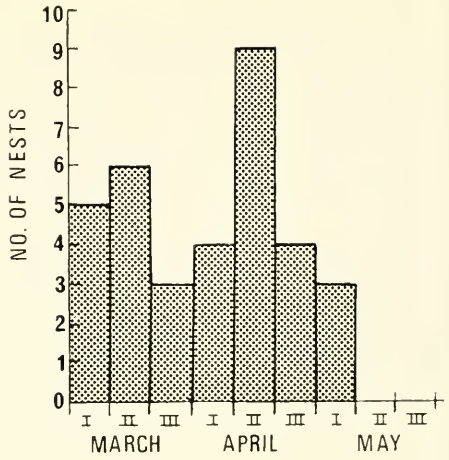

FIG. 14. Histogram of the breeding schedule of the Horned Lark in western Kansas. For explanation, see caption to Figure 11.

Rough-winged Swallow *Stelgidopteryx-ruficollis*. Moderately common summer resident. Nests solitarily or in small groups in sand banks along creeks and rivers (not necessarily those carrying surface water); nests placed 3-15′ high and 1.5-2.5′ deep in banks; 6(5.3,4-6;3) eggs are laid late May–early June.

Barn Swallow *Hirundo-rustica*. Common summer resident throughout. Nests solitarily or in small colonies in abandoned buildings or under bridges and rock outcroppings; nests placed 8.8′ (4-20;21) high; 4(4.6,4-6;9) eggs are laid late April–August (mostly May and early June).

Cliff Swallow *Petrochelidon-pyrrhonota*. Common summer resident throughout, especially in northwest and along Cimarron River. Nests in small to large colonies under bridges, culvert pipes, rock ledges, or in old buildings; 4-7 eggs are laid mid-May–mid-June.

Purple Martin *Progne-subis*. Local summer resident in urban areas. Nests in

"martin houses" in Scott, Ford, and Stevens counties; Wolfe (1961) states that martins nested commonly at the turn of the century in Oberlin, Decatur County, in crevices in buildings.

Blue Jay *Cyanocitta-cristata*. Present in woodlands throughout, but notably scarce in extreme southwest. Nests are placed in trees (*Populus*, *Acer*), 15.6′ (9-25;5) high; 5(5.3,5-6;3) eggs are laid late May–mid-June.

Black-billed Magpie *Pica-pica*. Present throughout, in open country, often near open woodlands. Density increases toward western edge of state. Apparently this magpie is extending its range eastward in Kansas. The species was not reported in Decatur County until 1918, and it is common there today (Wolfe, 1961); Linsdale (1927) found them only at Coolidge, Hamilton County, on his western trip in the summer of 1921; and Menke (1894) called them a "rare winter visitant" in Finney County, where they are common residents today. Nests are placed in trees (*Populus*, *Ulmus*, *Acer*, *Fraxinus*), 20.2′ (5-45;62) high; 7(7.0,7;3) eggs are laid mid-April–mid-June.

White-necked Raven *Corvus-cryptoleucus*. A regular but not common resident of high plains, generally away from river valleys; recorded from Comanche, Hodgeman, Scott, and Rawlins counties westward. Nests placed in windmill towers (21 records), isolated trees (*Populus*, *Ulmus*) away from streams and habitations (21 records), and telephone poles (5 records), 21.5′ (6-50;4) high; 7(6.0,4-7;4) eggs are laid late March–early May. Schwilling (1952) found 46 nests in 1951 in the following counties: Cheyenne (3), Finney (12), Greeley (1), Hamilton (4), Haskell (3), Hodgeman (4), Kearny (2), Rawlins (1), Scott (6), Sherman (5), Stanton (1), Thomas (2), Wallace (1), and Wichita (1).

Common Crow *Corvus-brachyrhynchos*. Common resident throughout, especially in river valleys but also recorded (not nesting) on high plains. Nests are placed in trees (*Populus*, *Tamarix*), 28.3′ (15-50; 3) high; perhaps 4 (only record) eggs are laid in late March (Ely and Thompson, 1971). Nesting records are from Comanche, Rawlins, Hamilton, and Meade counties.

Black-capped Chickadee *Parus-atricapillus*. Local summer resident in riparian woodlands from Arkansas River Valley northward. One record of a breeding bird, a male (KU 59639) taken in Seward County that was apparently mated to a *P.-carolinensis* (which see) (Rising, 1968). Graber and Graber (1951) collected this species in Meade and Morton counties, but the dates of collection (15 February, and 4 and 7 April, respectively) leave open the possibility that these individuals were non-breeding wanderers. Nests doubtless placed in cavities in trees; one nest (Decatur County) contained 5 eggs; eggs laid mid-April–early May. Nesting records are from Ford, Edwards, and Decatur counties.

Carolina Chickadee *Parus-carolinensis*. Local resident in woodlands and thickets along the Cimarron River, and (in Comanche County) in *Juniperus* woodlands in canyons; fairly common in Comanche and Clark counties (Rising, 1965a) but scarce in Meade and Seward counties. Westernmost record is of a female (KU 59640) apparently mated to a male *P.-atricapillus*, taken 10 mi NNE Liberal, Seward County, 6 May 1967 (Rising, 1968). This species may well be extending its range in Kansas as Goss (1891) makes no mention of it even though he worked extensively and lived in south-

central Kansas where they are common today.

House Wren *Troglodytes-aedon*. Common summer resident throughout, in riparian woodlands and thickets; highest densities in northwest, decreasing southward (where House Wrens may be "replaced" to some extent by Bewick Wrens [Table 3]). Nests are placed in natural cavities or abandoned woodpecker holes in trees (*Salix*, *Populus*, *Fraxinus*, *Acer*, fence post), 11.1′ (2.5-30;7) high; 6(5.3, 4-6;3) eggs are laid mid-May–early July (peak late May along the Cimarron River, early June along Republican River).

Bewick Wren *Thryomanes-bewickii*. Summer resident from Arkansas River southward, in riparian woodlands and thickets. Common along Cimarron River; not reported north or west of Dodge City or Ford, Ford County. Nests in crevices, 5′ (one record) high; 5(5.3,5-6;3) eggs are laid early May–mid-June. Nesting records from Comanche and Stevens counties.

Rock Wren *Salpinctes-obsoletus*. Summer resident throughout, in badlands, cliffs, and arid rocky outcroppings. Especially common in Cretaceous chalk in Gove, Scott, and Logan counties. Numbers appear to fluctuate from year to year (J. C. Barlow, pers. comm.). Nests in crevices in cliffs, rocks; 4(5.0,4-7;6) eggs are laid mid-May–mid-July (strong peak in mid-June [Fig. 15]). Nesting records from Comanche, Morton, Scott, Hamilton, Logan, and Decatur counties, and east to Rooks County (Imler, 1936). Cowbird parasitism is apparently heavy. Friedmann (1963) mentions 14 parasitized nests from Decatur County alone, and one parasitized nest has been reported from Scott County.

Mockingbird *Mimus-polyglottos*. Common summer resident in short open woodland; highest densities found along Cimarron River (Table 3). Nests in a variety of trees (*Tamarix*, *Populus*, *Salix*, locust, *Juniperus*), 9.4′ (2.5-30;11) high; 4(3.9, 3-4;8) eggs are laid early May–late June (Fig. 16).

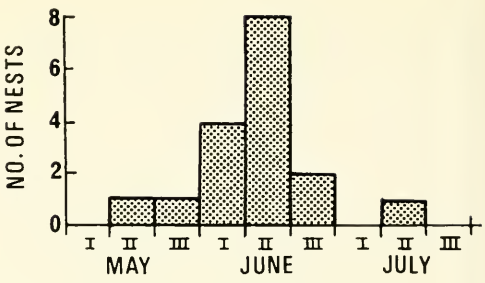

FIG. 15. Histogram of the breeding schedule of the Rock Wren in western Kansas. For explanation, see caption to Figure 11.

Catbird *Dumetella-carolinensis*. Local summer resident in rank riparian thickets, in extreme northwest and Ford County. Wolfe (1961) considered it "a rather common summer resident" in Decatur County (1908-1915), yet Tiemeier (1942) found but one individual in a week (27 July-1 August 1936) along Beaver Creek, Rawlins County. I found two pairs along Beaver Creek, 5 mi NE Atwood, Rawlins County, 8-12 June 1966, and saw one pair 9 mi W Dodge City, Ford County, 13 June 1966, and one 6 mi E Ford, Ford County, 3 June 1967. Imler (1936) considered the Catbird to be a "fairly com-

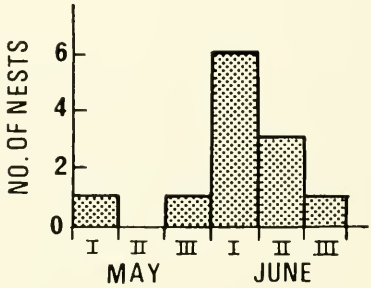

FIG. 16. Histogram of the breeding schedule of the Mockingbird in western Kansas. For explanation, see caption to Figure 11.

mon summer resident" in Rooks County, east of the region covered by this report. No definite nesting records are available.

Brown Thrasher *Toxostoma-rufum*. Summer resident throughout, in rank riparian brush; lowest density in southwest. Nests in bushes and small trees, often understory growth (*Populus*, *Salix*, *Prunus*), 4.0′ (2.5-7;6) high; 4(4.1,3-5;7) eggs are laid early May–early July.

Sage Thrasher *Oreoscoptes-montanus*. One record: a juvenile was taken (KU 41709) 7 mi N, 2 mi E Elkhart, Morton County, 17 July 1963 (Johnston, 1963).

Robin *Turdus-migratorius*. Virtually restricted to urban areas, but found in low density in woodlands along the Republican River, Cheyenne County. The spread of this species as a breeding bird through Kansas must have been very rapid following the settlement of the state. Allen (1872a, 1872b) spent two months in the state during 1871, stopping at Leavenworth, Leavenworth County, Topeka, Shawnee County, and Ft. Hays, Ellis County. A pair of Robins that he found at Topeka, where they were said to be "scarce" (Allen, 1872a), were the only individuals of this species that he found in Kansas. However, Wolfe (1961) considered Robins "a common summer resident" in Decatur County by 1908-15, Linsdale (1927) found them breeding at Garden City, Finney County, and Coolidge, Hamilton County, in June 1921, and Imler (1936) called them an "abundant summer resident" in Rooks County (based primarily on observations made 1935-1936). On 10-11 May 1968, J. A. Jackson and I found Robins breeding commonly along the Cimarron River in Union County, New Mexico, 10 mi W Kenton, Oklahoma. There we found two nests placed in *Tamarix* and one in *Populus*. This species, however, apparently does not breed in similar sites down stream in southwestern Kansas. Nests placed in trees (*Ulmus*), 18.3′ (12-30;3) high; 4 eggs (one record) are laid mid-April–early May.

Wood Thrush *Hylocichla-mustelina*. Low density summer resident in northwest. Wolfe (1961) found *H.-mustelina* to be an "uncommon summer resident" in Decatur County (1908-1915). He further writes: "One or more nests were observed nearly every year in the timber along Prairie Dog or Sappa creek; nesting began in early June." I have found this species once in northwestern Kansas, an individual seen along Beaver Creek, 5 mi NE Atwood, Rawlins County, 12 June 1966. S. A. Rohwer and I found a pair 2 mi S Kinsley, Edwards County, 10 May 1968; one of these sang persistently all morning and these birds may have nested in the rank *Populus-Salix-Tamarix* thickets there.

Swainson Thrush *Hylocichla-ustulata*. Fairly common throughout, especially in *Morus* shelterbelts, through mid-June; it is the commonest *Catharus* in western Kansas.

Gray-cheeked Thrush *Hylocichla-minima*. I have three June records of this species from western Kansas: 9 mi N, 7 mi W Hugoton, Stevens County, 10 June 1965; 1 mi SW Coolidge, Hamilton County, 15 June 1965 (specimen KU 49268, taken from *Maclura-Morus* shelterbelt) (Rising, 1965a); 3 mi N Sharon Springs, Wallace County, 27 June 1965, in riparian *Populus*.

Eastern Bluebird *Sialia-sialis*. Moderately common throughout, in open woodlands near water. Nests placed in abandoned woodpecker holes or natural cavities in trees (*Salix*, *Populus*, fence posts), 6.7′ (6-8;3) high; eggs are laid in April.

Mountain Bluebird *Sialia-currucoides*. Possibly a low density summer resident. A full-grown juvenile was taken (KU 5900) near Coolidge, Hamilton County, 20 June 1911, and an adult male (testis 12 × 8 mm) was taken (KU 32576) 1 mi W Pierceville, "Stanton" [*sic* = Finney] County, 5 June 1955 (Schwilling, 1956). This species is common in western Kansas during the winter.

Blue-gray Gnatcatcher *Polioptila-caerulea*. Low density, possibly eruptive summer resident in deciduous brush near water. Rising (1965a) found gnatcatchers in Grant, Morton, Finney, Ford, Logan, and Wallace counties in the summer of 1965, and this species was seemingly breeding at all those sites that summer. One breeding pair was taken in Morton County (KU 49270, 49271) at that time. A gnatcatcher was seen in Morton County, 19 August 1954 (Schwilling 1954).

Cedar Waxwing *Bombycilla-cedrorum*. Occasionally seen in small flocks in June, especially along the Arkansas River.

Loggerhead Shrike *Lanius-ludovicianus*. Fairly common summer resident, at least south of the Smoky Hill River Valley, in open country. Wherever *Prunus* are common, these birds seem to prefer these thickets. Apparently rare in extreme northwest. Wolfe (1961) writes: "Extremely rare; only two nests were ever observed and these in different years," in commenting on the status in Decatur County. One definite nesting record from Ford County (date not available); numerous summer sightings from Comanche, Clark, Ford, Edwards, Stanton, Morton, Meade, Haskell, Finney, Hamilton, Gove, and Logan counties.

Starling *Sturnus-vulgaris*. Common summer resident throughout, especially in riparian *Populus* woodlands. As this introduced bird did not appear in eastern Kansas until the 1930s (Johnston, 1964), it is not mentioned in the early accounts of the avifauna of the west. Imler (1936) does not mention the species in his list from Rooks County, indicating that Starlings had not dispersed to that County by 1936. The Grabers (1951) do not mention Starlings among those species recorded from southwestern Kansas in 1950; they are common there today. In 1965, as I collected throughout western Kansas, I found Starlings only in Meade, Hamilton, and Finney counties, and they were common only in the latter two. By 1967 I found them nesting commonly west to 10 mi NNE Liberal, Seward County, along the Cimarron River, and in low density as far west as Hugoton, Stevens County, and also found them breeding at Ford, Ford County, St. Francis, Cheyenne County (common), Sharon Springs, Wallace County, and in Logan County. In the spring of 1968 they were breeding along the Cimarron River north of Elkhart, Morton County, and as far west as 10 mi W Kenton, Oklahoma, in Union County, New Mexico. Nests are placed in abandoned woodpecker holes or other cavities in trees (*Populus*, *Ulmus*), 10-40′ high; 6 eggs (only record) are laid mid-April–mid-June.

Black-capped Vireo *Vireo-atricapilla*. Formerly a local summer resident in scrub woodland, at least in Comanche County. Goss (1885b) found a nest under construction 5′ high in *Ulmus* there, 11 May 1885, and obtained 4 specimens. This species almost certainly no longer occurs in Kansas (J. C. Barlow, pers. comm.).

Bell Vireo *Vireo-bellii*. Local and generally uncommon summer resident in deciduous thickets (*Prunus, Salix, Salix-Tamarix*). Greatest densities along the Cimarron River west to Stevens County,

and in Ford County (Table 3). Tiemeier (1942) reports that *V.-bellii* was common at Ludell, Rawlins County, in 1936, but I failed to find it there either in 1965 or in 1966. Wolfe (1961) lists *V.-bellii* as a "common summer resident" in suitable habitat in Decatur County at the turn of the century; Linsdale (1927) found a singing bird at Coolidge, Hamilton County, 15 July 1921. I have found them north to Sheridan and Rawlins counties. Nests in deciduous bushes or thickets (*Prunus*), 1.5′ high (only record); 3 or 4 eggs are laid in early June in Decatur County. Parasitism by cowbirds probably common. Wolfe (1961) found "nearly every nest" parasitized.

Red-eyed Vireo *Vireo-olivaceus*. Rare or local summer resident in open *Populus* woodlands. Wolfe (1961) considered it "very rare" in Decatur County, where he found it nesting but once in the early 1900s. Graber and Graber (1951) collected two males that may have been breeding in Morton County (19 and 20 May 1950). I have seen this species at four localities: 17 mi E Coldwater, Comanche County, 18 July 1964; 9 mi N, 7 mi W Hugoton, Stevens County, 10 June 1965; 14 mi W, 18 mi S WaKeeney, Trego County, 21 June 1965; 7.5 mi N, 3 mi W Elkhart, Morton County, 4 July 1966.

Warbling Vireo *Vireo-gilvus*. Occurs in tall *Populus* throughout, in moderate density in southwest and in low density in northwest (Table 3). Wolfe (1961) considered *V.-gilvus* a "rare summer resident" in Decatur County. Nests placed 3′ and 25′ in *Prunus* and *Populus*, respectively; 3 eggs (only record) laid mid-June in Decatur County.

Yellow Warbler *Dendroica-petechia*. Summer resident in riparian *Populus-Salix* woodlands; highest densities in southwestern counties (Table 3), increasing toward west; they are quite common along the Cimarron River in Union County, New Mexico. Wolfe (1961) and Menke (1894) call *D.-petechia* an abundant summer resident in Decatur and Finney counties, respectively; Linsdale (1927) found Yellow Warblers along the Arkansas River at Coolidge, Hamilton County. Nests in rank deciduous brush (*Populus*, *Salix*, *Tamarix*), maybe 20′ (only record) high; 4(4.0,4;3) eggs are laid late May–mid-June. Wolfe (1961) states that Yellow Warblers are common hosts of the cowbird in Decatur County. Nesting records are from Decatur, Stevens, and Morton counties.

Blackburnian Warbler *Dendroica-fusca*. One June record: male, KU 57782, taken 6 mi E Ford, Ford County, 2 June 1967, not in breeding condition.

Blackpoll Warbler *Dendroica-striata*. One June record: KU 53072, taken 5 mi NE Atwood, Rawlins County, 11 June 1966, not in breeding condition.

Louisiana Waterthrush *Seiurus-motacilla*. Only one record of breeding: Wolfe (1961) found a nest containing three young under an overhanging bank approximately 3′ above Sappa Creek, east of Oberlin, Decatur County, 10 June 1910.

Yellowthroat *Geothlypis-trichas*. Low density summer resident throughout, in wet, rank, low thickets (*Salix*, *Tamarix*, *Typha*). No nesting data are available.

Yellow-breasted Chat *Icteria-virens*. Locally common summer resident in rank, tall riparian growth (*Salix*, *Tamarix*, other). Wolfe (1961) considered them "not uncommon" in Decatur County; Tiemeier (1942) found them "common" in Rawlins County, as I have. Menke (1894) found them "common" in Finney County, and Linsdale (1927) found "several" in *Salix* at Coolidge, Hamilton

County, 15 July 1921. Only two nesting records are available: one, a nest containing a cowbird egg, in Decatur County, 22 June 1908 (Friedmann, 1963); another, a female incubating eggs, 3′ in "current bush," in Finney County, 27 June 1951.

House Sparrow *Passer-domesticus*. Common resident throughout, in urban areas and around agrarian developments. Present in western Kansas at least by the 1890s. Menke (1894) writes: "Resident; and I am sorry to say abundant." Nests placed in niches in buildings, farm machinery, abandoned bird nests (*Corvus*, *Pica*, *Petrochelidon*), or woven in trees (*Ulmus*, *Populus*); 4-5(4.5,4-5;4) eggs are laid.

Eastern Meadowlark *Sturnella-magna*. Known only from Comanche and Edwards counties where they are fairly common during the summer. *S.-magna* may be expanding its range westward into southwestern Kansas as I did not record it there until 1968 (although I could easily have overlooked it on earlier trips). No nesting data are available.

Western Meadowlark *Sturnella-neglecta*. Common throughout, in open country. Nests placed on ground, under a tuft of grass; 4(3.7,3-4;3) eggs are laid in late May.

Yellow-headed Blackbird *Xanthocephalus-xanthocephalus*. Local, uncommon, and colonial summer resident, in emergent vegetation in deep permanent marshes. Goss (1891) found a colony nesting along Crooked Creek, Meade County, 1 June 1885, and he (1885a) saw a flock at Wallace, Wallace County, 26 June 1884. Linsdale (1927) saw flocks of Yellow-headed Blackbirds in Kearny, Hamilton, and Gove counties in July 1921. Johnston (1964) mentions nesting in Meade and Wallace counties (probably Goss' records). Yellow-headed Blackbirds were perhaps formerly more common in western Kansas; I have not seen this species there during the breeding season.

Red-winged Blackbird *Agelaius-phoeniceus*. Common, colonial summer resident, near water. Nests placed in rank deciduous vegetation (*Salix*, *Tamarix*, *Ambrosia*, "bush") near water or (more commonly) in emergent vegetation (*Typha*, "reeds"), 2.3′ (0.5-6;33) high; 4(4.0,3-5;33) eggs are laid early May–early July; great latitude in breeding season (Fig. 17) may reflect extreme local seasonal variability in marsh conditions. Wolfe (*in* Friedmann, 1963) states that "probably 90 percent of the redwing nests [from Decatur County] contained one or more eggs of the cowbird. . . ." These are, however, the only records of such parasitism from western Kansas.

Orchard Oriole *Icterus-spurius*. Common summer resident throughout, in rank *Salix* and/or *Populus*; density lower at western edge of state (Table 3). Nests suspended from trees (*Populus*, probably *Salix*), 35.7′ (12-55;3) high; 4(4.4,4-5;14)

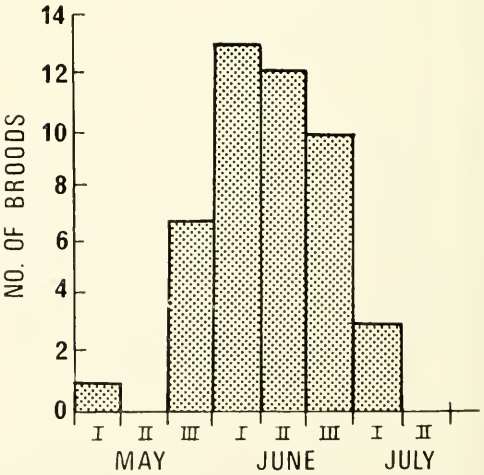

FIG. 17. Histogram of the breeding schedule of the Red-winged Blackbird in western Kansas. For explanation, see caption to Figure 11.

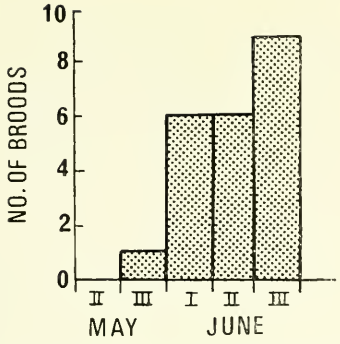

Fig. 18. Histogram of the breeding schedule of the Orchard Oriole in western Kansas. For explanation, see caption to Figure 11.

eggs are laid late May–late June (Fig. 18); no records of cowbird parasitism are available.

Baltimore/Bullock orioles *Icterus-galbula/Icterus-bullockii*. Abundant throughout, in trees. These two morphs, considered to be one species by many, occur in woodlands (esp. *Populus*) throughout (Rising, 1970; Table 3). The Baltimore is the conspicuous morph in the east, west to Clark, Ford, Gove, Sheridan, and Rawlins counties; the Bullock is dominant in Stevens, Morton, Kearny, Hamilton, and Wallace counties. A variety of individuals intermediate between the Baltimore and Bullock types occur throughout, and such birds are the majority in Meade, Seward, Finney, Scott, Logan, and Cheyenne counties (Figs. 8-9). The previous status of these orioles in western Kansas is enigmatic: Allen (1872a) found *I.-galbula* "Common in the timber" in Ellis County in 1871, and found *I.-bullockii* at Cheyenne, Wyoming, and at Huntsville (near Denver), Colorado (although he incorrectly identified these as *I.-galbula*), at that time; on the other hand Menke (1894) considered *I.-galbula* to be a "rare summer resident" in Finney County in the 1890s, and does not mention *I.-bullockii* (which he possibly did not separate from *I.-galbula*) in his account of the avifauna of that county. Both morphs and intermediate individuals are common in Finney County today. Because of the near impossibility of segregating nesting data from this area as to morph-type, they are presented together here. Nests suspended from trees (primarily *Populus*; rarely *Ulmus*, *Quercus* sp., telegraph pole [Linsdale, 1927]), 25.0′ (8-50;37) high; 5(4.7,4-5;57) eggs are laid mid-May–late June (Fig. 19); no records of cowbird parasitism are available.

Brewer Blackbird *Euphagus-cyanocephalus*. Goss (1891) states that this species is ". . . an occasional resident in the western part of the state." At the present time there is no other evidence that Brewer Blackbirds occur in western Kansas during the summer months, although they are common there in migration.

Common Grackle *Quiscalus-quiscula*. Locally common summer resident, near water. Most frequently seen in groves of trees adjacent to farm houses, and in towns. Highest densities seemingly in northwest. Nests in trees (*Salix*, *Populus*, *Ulmus*), 19.4′ (12-30;5) high; 4 (only record) eggs laid in May. Allen (1872b)

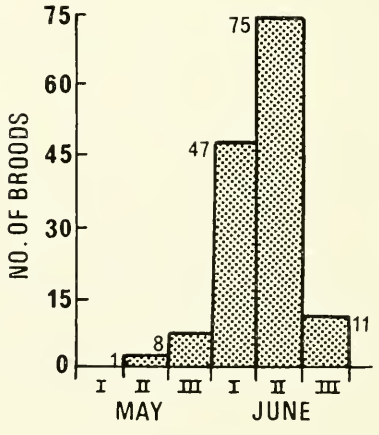

Fig. 19. Histogram of the combined breeding schedules of Baltimore and Bullock orioles, and intermediates between them, in western Kansas. For explanation, see caption to Figure 11.

mentions a nest placed in an abandoned woodpecker hole in Ellis County, east of the region covered by this paper.

Brown-headed Cowbird *Molothrus-ater*. Common summer resident throughout, in woodlands and edge. Eggs of *M.-ater* have been found in the nests of the following species in western Kansas: Say Phoebe, Rock Wren, Bell Vireo, Yellow Warbler, Yellow-breasted Chat, Red-winged Blackbird, Black-headed Grosbeak, Grasshopper Sparrow, and Lark Sparrow. However, in addition to these, the following species are doubtless suitable hosts for cowbirds in this region: Western Meadowlark, Cardinal, Indigo Bunting, Blue Grosbeak, Dickcissel, Lark Bunting, and Cassin Sparrow. Although a large porportion of the nests of the phoebe, wren, vireo, and Yellow Warbler are parasitized by *M.-ater*, these species are either so uncommon or local that they cannot be significant as hosts for cowbirds in western Kansas.

Cardinal *Richmondena-cardinalis*. Low density, local summer resident west of Seward, Hamilton (Graber and Graber, 1951), and Cheyenne counties; moderately common in Comanche, Clark, Seward, Finney, Ford, Sheridan, Rawlins, and Decatur counties. Nests are placed in rank vegetation (*Salix*, *Juniperus*, vines), 6-7′ high; 3-5(4.0,3-5;3) eggs are laid early May–early June. Nesting records are from Ford, Seward, and Comanche counties. Another species that is probably extending its range westward along trans-plains watercourses, the Cardinal is not mentioned in any of the early lists for this region. Tiemeier (1942) found them "fairly common" in Rawlins County in 1936.

Rose-breasted Grosbeak *Pheucticus-ludovicianus*. Tiemeier (1942) took one specimen of an adult male (KU 21523) 2 mi NE Ludell, Rawlins County, 28 July 1936. West (1962) correctly points out that this specimen (adult male) is phenetically intermediate between *P.-ludovicianus* and *P.-melanocephalus*. Nonetheless, the *P.-ludovicianus* morph probably occurs in low density in Decatur and Rawlins counties.

Black-headed Grosbeak *Pheucticus-melanocephalus*. Most specimens and records of *Pheucticus* from western Kansas are of the *P.-melanocephalus* morph. Menke (1894) considered it a "rare summer resident" in Finney County in the 1890s; Linsdale (1927) found them at Coolidge, Hamilton County, and Gove County, in July 1921; Wolfe (1961) found them "Fairly common as a summer resident nesting in early June . . ." in Decatur County; and Tiemeier (1942) found them common in Rawlins County in July 1936. I have found *P.-melanocephalus* commonly in Decatur, Rawlins, and Cheyenne counties in mixed deciduous woodlands (*Fraxinus*, *Acer*, *Morus*, *Populus*). Specimens and records from extreme southwest, from early summer, are probably all of transient individuals: Graber and Graber (1951), two specimens (25 and 26 May); specimen (KU 57869) of a first-year male taken 10 mi N, 8 mi W Hugoton, Stevens County, 7 June 1967; common 10 mi NNE Liberal, Seward County, 5-6 May 1967. Nests in *Prunus* and *Acer*, perhaps 6′ (only record) high; 3-4 eggs laid late May–early June. Two incidences of cowbird parasitism (Friedmann, 1963). All definite nesting records from Decatur County.

Blue Grosbeak *Guiraca-caerulea*. Common summer resident throughout, in rank riparian thickets. Nests placed in a variety of trees (*Populus*, *Salix*, *Juniperus*), 7 and 10′ high; 5 (only record) eggs are laid late May–mid-July (most records mid-June–mid-July).

Indigo Bunting *Passerina-cyanea*. Uncommon or local summer resident in riparian thickets throughout; locally moderately common in Comanche, Clark, and Ford counties. Although Menke's (1894) mention of this species in Finney County (as a rare summer resident) is unique among early lists, I have found this species in Comanche (18 July 1964), Clark (6 June 1965), Seward (9 July 1965), Stevens (6 June 1967*), Morton (22 June 1968*; 13 July 1964*), Ford (13 June 1966; 18 June 1965), Hamilton (15 July 1964*), Sheridan (8 August 1966*), Wallace (17 June 1967), and Cheyenne (15 June 1967*) counties. The six specimens taken (asterisks) all appear to be of typical *P.-cyanea*; they are in the collection at The University of Kansas.

Lazuli Bunting *Passerina-amoena*. Menke (1894) called this species a "common summer resident" in Finney County, but details no incident of nesting. The Grabers (1951) found Lazuli Buntings commonly in Morton and Hamilton counties in May 1950, and collected two females with "enlarged ovaries" in Morton County, 20 and 27 May. Thompson (1958) gives a definite nesting record, a nest containing one egg found 8.5 mi N Elkhart, Morton County, 4′ high in white sweet clover, 18 July 1958. This species and the preceding are both likely of eruptive occurrence in the far western counties.

Painted Bunting *Passerina-ciris*. A locally common summer resident in *Salix-Tamarix* thickets and rank shelter-belts, in Comanche and Clark counties. One specimen taken 10 mi N, 8 mi W Hugoton, Stevens County, 7 June 1967, was apparently a first-year female not yet in breeding condition. One record of adults feeding young out of the nest in June 1964, in Ford County, is the only definite nesting record.

Dickcissel *Spiza-americana*. Locally common summer resident in rank weedy meadows, alfalfa fields, clover, near water. Nests about 1.5′ high (only record), in annual vegetation (alfalfa); 3(3.0,3;3) eggs are laid in June. Nesting records from Morton, Logan, and Decatur counties.

American Goldfinch *Spinus-tristis*. Moderately common summer resident throughout, in woodlands and edge. One nesting record: 5 eggs (incubation begun), 8′ high in *Prunus*, Decatur County, 21 August 1911.

Rufous-sided Towhee *Pipilo-erythrophthalmus*. Low density summer resident in Decatur, Rawlins, and Comanche counties, in rank riparian thickets. Rising and Anderson (1964) took an adult male (KU 41508) 2 mi E, 1 mi N Oberlin, Decatur County, 27 July 1963, that was feeding fledged young. I saw an adult male 5 mi NE Atwood, Rawlins County, 10 June 1967, and two males along Bluff Creek, 17 mi S, 6 mi W Coldwater, Comanche County, 12 May 1968. The Decatur County specimen is intermediate in back-spotting between "spotted" and "unspotted" morphs in *P.-erythrophthalmus*, whereas the two seen in Comanche County seemed "spotted."

Lark Bunting *Calamospiza-melanocorys*. Found throughout, in open country. Density moderate in Comanche, Clark, eastern Ford, and Rawlins counties, increasing westward. Highest densities along Arkansas and Smoky Hill rivers, in Hamilton, Scott, Gove, and Logan counties. Abundance and distribution may vary considerably from year to year (Goss, 1891). Nests placed on the ground at the base of a clump of vegetation (volunteer wheat); 4(4.3,4-5;6) eggs are laid late May–late June (Fig. 20). Nesting records

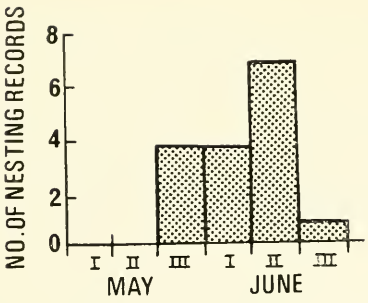

FIG. 20. Histogram of the breeding schedule of the Lark Bunting in western Kansas. For explanation, see caption to Figure 11.

are from Ford, Gray, Meade, Scott, and Logan counties.

Grasshopper Sparrow *Ammodramus-savannarum*. Summer resident throughout, in shortgrass prairie and sand hills. Fairly common to common in Comanche, Edwards, Ford, Meade, Finney, Gove, Logan, and Decatur counties, decreasing in density westward, especially toward the extreme corners of the state. Nests placed on ground, in shortgrass; 4(4.3,4-5;3) eggs are laid late May–mid-June (three records). One incidence of cowbird parasitism (Decatur County; Friedmann, 1934). Nesting records are from Scott, Seward, Ford, Morton, and Decatur counties.

Vesper Sparrow *Pooecetes-gramineus*. One record: an adult male, KU 41778, taken 7.5 mi N Elkhart, Morton County, 17 July 1963, that may have been a breeding bird (Johnston, 1963). The species is abundant in migration in western Kansas.

Lark Sparrow *Chondestes-grammacus*. An abundant summer resident throughout, in woodland edge and medium grassland interspersed with shrubs. Nests placed on ground at the bases of plants (grasses, thistles, mallows) or rocks, or in trees (*Populus*, *Juniperus*); 5(4.3,3-5;13) eggs are laid mid-May–early July (Fig. 21); clutch-size of nests placed on ground seems larger [5(4.7,4-5;10)] than that of those placed in trees [3(3.0,3;3)], and this difference appears to be independent of season. One incidence of cowbird parasitism from Meade County, and nine records from Decatur County (Friedmann, 1934).

Rufous-crowned Sparrow *Aimophila-ruficeps*. Perhaps a local and irregular summer resident in extreme south. One specimen (KU 29222) from Schwartz Canyon, Comanche County, 7 June 1936 (Johnston, 1960); the Grabers (1951) saw one near Point Rock, Morton County, 21 May 1950.

Cassin Sparrow *Aimophila-cassinii*. Common virtually throughout, in sagebrush-grassland. In northern tier of counties, recorded only in Cheyenne County. Nests in sage, probably at bases of or low in plants; 4(3.8,3-4;4) eggs are laid mid-May–mid-July (7 records), the temporal latitude suggesting two broods or much inter-seasonal variation. Nesting records are from Morton, Finney, Seward, Stevens, and Logan counties.

Chipping Sparrow *Spizella-passerina*. An individual seen 12 mi NE Liberal, Seward County, 9 July 1965, was doubtless a transient. The species is a common transient in western Kansas.

Clay-colored Sparrow *Spizella-pallida*. The sight record of two adult and three

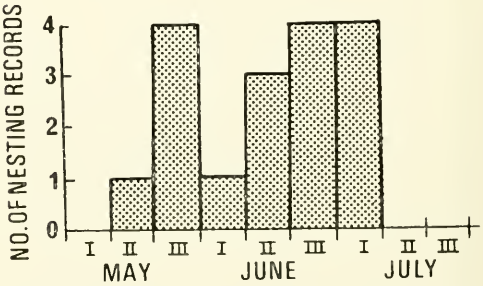

FIG. 21. Histogram of the breeding schedule of the Lark Sparrow in western Kansas. For explanation, see caption to Figure 11.

young Clay-colored Sparrows 3 mi N, 2 mi W Elkhart, Morton County, 4 September 1964 (Trautman, 1964), is strong evidence of low density breeding in that sector. No other record is available.

Brewer Sparrow *Spizella-breweri*. A sighting from 7 mi N, 2 mi E Elkhart, Morton County, 17 July 1963 (Easterla, 1964), is the only record of this species from western Kansas during the nesting season. The species is common in migration.

Field Sparrow *Spizella-pusilla*. A locally common summer resident in Comanche, Clark, and Finney counties, especially in *Prunus* thickets but also in woodland edge. I collected a male, KU 45634, 18 July 1964, with large testes (10 × 6 mm) and protruding cloaca, 17 mi E Coldwater, Comanche County, that was doubtless breeding, but no nest nor laying female has been taken.

Lincoln Sparrow *Melospiza-lincolnii*. An indvidual seen 6 mi E Ford, Ford County, 5 June 1967, was doubtless a transient.

Chestnut-collared Longspur *Calcarius-ornatus*. Probably formerly a locally common summer resident, at least in the vicinity of Ellis, Trego, Gove, and Logan counties. Allen (1872a) found them common in the vicinity of Ft. Hays, Ellis County. There he collected 30 specimens and 3 full sets of eggs (clutch-size was "generally five") in June, 1871. There are no modern records. The nest, as described by Allen, ". . . is a very neat, though slight structure, placed of course on the ground, and is composed of dry fine grass and rootlets. . . . Full sets of freshly laid eggs were first found about June 3rd." In another paper (1872b) Allen comments they ". . . were only met with on the high ridges and dry plateaus, where they seemed to live somewhat in colonies. At a few localities they were always numerous, but elsewhere were often not met with in a whole day's drive."

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